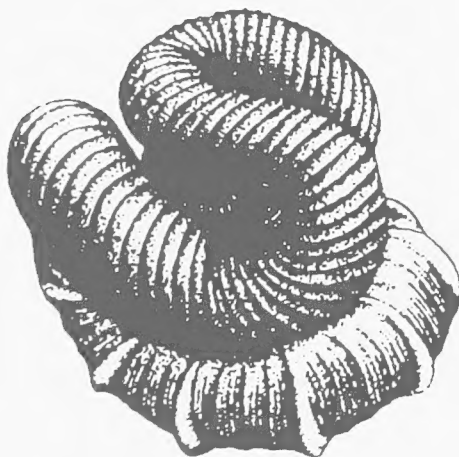


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Cover : Idealized sketch of *Nipponites mirabilis* Yabe, a Late Cretaceous (Turonian) nostoceratid ammonite. Various reconstructions of the mode of life of this species have been proposed, because of its curiously meandering shell form (after T. Okamoto, 1988).

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Permian bivalves from West Spitsbergen, Svalbard Islands, Norway

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Abstract. The bivalve fossils collected by Japanese-Norwegian research groups from the Kapp Starostin Formation in west Spitsbergen are described. They comprise fourteen species belonging to the Pterioda and two species of the Arcoida. Among them, six species, including two that are indeterminate, are newly described. They are *Grammatodon* (*Cosmetodon*)? *suzukii*, G. (C.)? sp. ind., *Streblochondria winsnesi*, *Vorkutopecten svalbardensis*, *Deltopecten* sp. ind., and *Palaeolima nakamurai*. The fauna belongs to the Boreal bioprovince, but a single species, *Cassianoides sexcostatus* (Stuckenberga) has also been reported from the Central Rocky Mountains of the United States. The bivalve fauna suggests an Artinskian-Kungurian age for the Kapp Starostin Formation. This is somewhat earlier than the age deduced from brachiopods and bryozoans, but it is not decisive because the materials are poor. The Kapp Starostin Formation is conformably overlain by the *Otoceras*-bearing, earliest Triassic Vardebukta Formation, so a time-gap corresponding at least to the Dorashamian and Dzhulfian (=Tatarian) is inferred between the two formations.

Key words: Kapp Starostin Formation, Permian bivalves, Spitsbergen

Introduction

The study materials were collected by Nakamura *et al.* in 1984 and 1990, and by Nakazawa *et al.* in 1986 from the Permian Kapp Starostin Formation of west Spitsbergen, in the Svalbard Islands, Norway. Brachiopods and bryozoans are most abundant among the macrofossils. Many species of brachiopods have been described by various authors, notably, Frebold (1937) and Gobbet (1963). Bivalves are found rather rarely and the descriptive studies are few. Toula (1873, 1875a, b) first described the following species, collected from "Carboniferous-Permian" strata on Sørkapp Island off the southern tip of Spitsbergen, and Axel Island in Bellsund and on Hornsund, on the west coast of Spitsbergen:

Pecten (*Aviculopecten*) *bouei* Verneuil, *Pecten* (*Aviculopecten*) *kokscharofi* Verneuil, *Pecten* (*Aviculopecten*) cf. *ellipticus* Phillips, *Pecten* (*Aviculopecten*) cf. *dissimilis* Fleming, *Pecten* (*Aviculopecten*) *wilczeki* Toula, *Gervillia* cf. *antiqua* Münster, *Aviculopecten draschei* Toula and *Gervillia* sp.

Frebold (1937) described the following species, mostly from the upper part of the Kapp Starostin Formation in the Festningen section, located on the southern coast of Spitsbergen at the entrance to Isfjorden and from Sørkapp Island:

Aviculopecten (*Deltopecten*) cf. *mutabilis* Licharew and A. (D.) cf. *hiemalis* Salter, *Aviculopecten*? sp. indet., *Pecten*

(*Aequipecten*)? *keyserlingiformis* Licharew, *Pecten* (*Aequipecten*) *keyserlingi* Stuckenberga, *Pecten* (*Pseudamysium*) cf. *ufaensis* Tschernyschew, *Pecten* (*Pseudamysium*) ex aff. *sericeus* Verneuil, *Parallelodon* sp. ind., genus [= *Parallelodon*?] et sp. ind., *Clidophorus*? sp. ind., *Pecten wilczeki* Toula, and *Leda* sp. ind.

Among the species described by Toula, *Aviculopecten bouei* was referred to *Aviculopecten* (*Deltopecten*) *mutabilis* by Licharew (1927). *Pecten* cf. *ellipticus* was identified as *Pecten* (*Pseudamysium*) ex aff. *sericeus* Verneuil, and *Pecten* (*Aviculopecten*) cf. *dissimilis* was compared to *Aviculopecten netschajewi* Licharew and reported as *Aviculopecten*? sp. ind. by Frebold (1937). *Aviculopecten kokscharofi* reported by Toula (1873) is probably identical with *Aviculopecten* cf. *hiemalis* illustrated by Licharew (1927, especially pl. 5, fig. 20), and is referred to *Etheripecten* cf. *mutabilis* Licharew in the present paper.

Among the species reported by Frebold, *Aequipecten keyserlingi* was considered to belong to the genus *Morrispecten* Muromtseva and Guskov by Muromtseva (1984, p. 75). *Morrispecten* is, however, a junior synonym of *Undopecten* Waterhouse, 1982 (Newell and Boyd, 1995). *Pecten* (*Aequipecten*)? *keyserlingiformis* and *Aviculopecten* (*Deltopecten*) cf. *mutabilis* and A. (D.) cf. *hiemalis* of Frebold are referred to *Etheripecten keyserlingiformis* and E. cf. *mutabilis*?, respectively. *Pseudamysium* cf. *ufaensis* and *Parallelodon* sp. ind. are identified as *Streblochondria winsnesi* sp. nov. and *Grammatodon* (*Cosmetodon*)? *suzukii* sp.

nov., respectively, in the present paper. Sixteen species including four new species and two indeterminable ones are described. All the materials are kept at the Department of Geology and Mineralogy, Faculty of Science, Kyoto University.

Stratigraphy

The fossils were collected at four localities in west Spitsbergen, namely, the Festningen section along the southern coast of the entrance to Isfjorden, the Skansbukta section at Billfjorden, and the Reinodden and Ahlstrandodden sections along the southern coast near the entrance of Van Keulen-fjorden, in Bellsund (Figure 1). Faunas from the first and second localities were collected on Nakamura's expedition in 1984 and in 1990. The stratigraphy of these sections was published by Nakamura *et al.* in 1990 and, in more detail, by the Japanese-Norwegian Research Group (1992). The other two localities were examined by Nakazawa's party in 1986 and the results were published by Nakazawa *et al.* (1990). All the materials are from the Permian Kapp Starostin Formation which was defined by Cutbill and Challinor (1965). The formation corresponds to the Brachiopod Cherts (including the *Spirifer* Limestone at the base) of previous authors (e.g., Gee *et al.*, 1953). At the type locality, Festningen, the formation is divided into three members, the Vøringen, Svenskeegga, and Hovtinden Members in ascending order (Cutbill and Challinor, 1965).

(1) Festningen section (Figure 2A)

At Festningen the Kapp Starostin Formation is 385 m in thickness and divided into twelve units (Nakamura *et al.*, 1990; Japanese-Norwegian Research Group, 1992). Unit 1, about 20 m thick, is represented by brachiopod-rich, bioclastic limestone beds corresponding to the Vøringen Member. Units 2 to 5, about 140 m thick, constitute the Svenskeegga Member, each represented mainly by siliceous shale, spicularite, spicularite and shale, and bioclastic limestone, respectively.

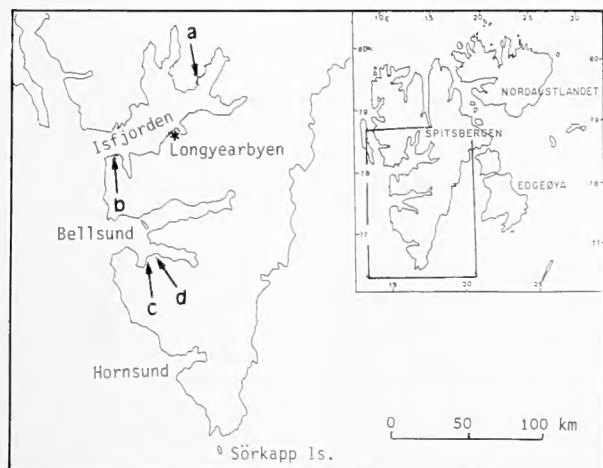


Figure 1. Map of southern Spitsbergen showing fossil localities. a: Skansbukta, b: Festningen, c: Reinodden, d: Ahlstrandodden.

The Hovtinden Member, about 225 m thick, consists of seven units, 6 to 12, each composed mainly of spicularite, alternation of spicularite and spicularitic shale, bioclastic limestone, spicularite, bioclastic limestone (partly silicified), alternation of siltstone and paper shales, and quartzose sandy shale or siltstone, respectively, in ascending order. Bivalve fossils have been obtained from Units 5, 7, 8, 9 and 11.

(2) Reinodden section (Figure 2B)

At Reinodden the formation reaches more than 300 m in thickness. It is classified into eight units, A to H, in ascending order (Nakazawa *et al.*, 1990). Unit A, less than 5 m thick, is the Vøringen Member consisting of fossiliferous bioclastic limestone. Units B and C are referred to the Svenskeegga Member. Unit B, about 40 m thick, is subdivided into three beds or subunits, 2 to 4. Beds 2 and 4 are represented by nodular or irregularly bedded, alternating spicularitic chert and thin mudstone. Bed 3 consists of black laminated shale and siltstone. Unit C, about 80 m thick, includes bedded black shale (Bed 5), and alternations of calcareous sandstone and limestone (Beds 6 and 7).

The Hovtinden Member (Units D to H), about 180 m thick, is characterized by coarse-grained sandstone and spicularite. It is subdivided into fourteen beds, Beds 8 to 21, as shown in Figure 2B. Glauconite is commonly found in the sandstones. Macrofossils have been collected from ten horizons (RP 1~10) in the Kapp Starostin Formation, among which RP 3, 7 and 9 contain bivalve fossils.

(3) Ahlstrandodden section (Figure 2C)

At Ahlstrandodden the formation is about 250 m thick. It is divided into eight units, 1 to 8 (Nakazawa *et al.*, 1990). Unit 1, 7.6 m thick, consists of brachiopod-rich bioclastic wackestone of the Vøringen Member. Units 2 and 3, which are 40 m and 58 m thick, respectively, are correlated to the Svenskeegga Member. Units 4 to 8, about 140 m thick altogether, correspond to the Hovtinden Member. They are composed mainly of spicularitic chert or spicularite, siliceous shale and a minor amount of limestone. Glauconite grains are commonly found in siliceous sandstones throughout the Hovtinden Member.

Among nine fossiliferous horizons (AP 1~9) within the formation, five horizons, AP 1, 2, 6, 7 and 8, yield bivalve shells. The fossiliferous horizons AP 8 and 9 of the upper part of the Hovtinden Member can be correlated with horizons RP 9 and 10 in the Reinodden section. They are considered to correspond to horizon F 8 of the Festningen section.

Fossil occurrence and age assignment

Sixteen species in nine genera are identified from three sections mentioned above, plus one species, *Acanthopecten licharewi* (Fredericks), from Skansbukta (SA 7), as shown in Figures 3. The localities and stratigraphic horizons are shown in Figure 2.

Nakamura *et al.* (1987, 1992) distinguished five brachiopod assemblage zones in the Kapp Starostin Formation of the Isfjorden area. They compared these faunas to those of Russia, Arctic Canada, Greenland, and Alaska, all belonging

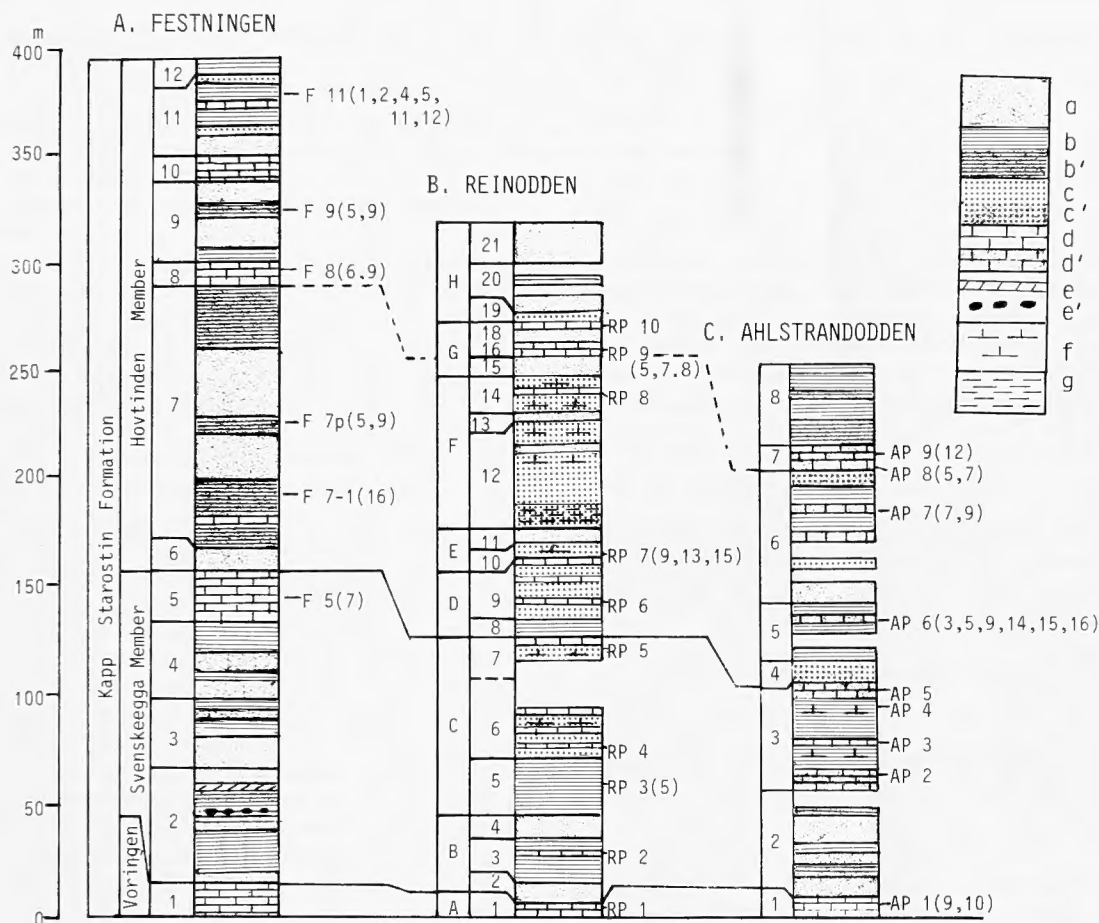


Figure 2. Geological columnar sections of the Kapp Starostin Formation at three localities showing horizons of macrofossils. a: chert or spicularite, b: shale or mudstone, b': siliceous or spicularitic, c: sandstone, c': siliceous, d: limestone, d': siliceous, e: dolostone, e': dolostone nodule, f: calcareous, g: muddy. Numbers in parentheses correspond to those of bivalve species in Figure 3. A: simplified from Japanese-Norwegian Research Group (1992, fig. 2), B and C: from Nakazawa *et al.* (1990, fig. 2).

to the Boreal bioprovince. From the correlation of these faunas, they concluded that the Kapp Starostin Formation ranges in age from Kungurian up to Midian or early Dzhulfian (Tatarian). Sakagami (1992) studied the bryozoans and pointed out the similarity of the fauna from the Vøringen Member with the Kungurian fauna in the Timan-Pechora region. Faunas of the Svenskeegga and Hovtinden Members resemble Ufimian faunas of Arctic Canada and the Russian Far East, the Kazanian fauna of the southern Urals, and the Late Permian fauna of British Columbia. These comparisons are consistent with the age range inferred from the brachiopods, except that there is no positive evidence, from the bryozoans, of the presence of Dzhulfian strata. These observations support previous views on the age of the Kapp Starostin Formation, for example, Forbes *et al.* (1958) and Flood *et al.* (1971).

The ranges of the bivalve species are shown in Figure 3. Only two species, *Vorkutopecten svalbardensis* and *V. aff. svalbardensis* have been found in the Vøringen Member. The overlying Svenskeegga Member is also poor in bivalves.

Five species have been collected there, namely, *Etheripecten* cf. *mutabilis*, *Etheripecten wilczeki*, *Vorkutopecten svalbardensis*, *Acanthopecten licharewi*, and *Deltotopecten* sp. All infrequently occur and their ranges extend up into the Hovtinden Member. Accordingly, the fauna is not essentially different from that of the Hovtinden Member.

Eight and ten species could be identified from the lower and upper parts of the Hovtinden Member, respectively. In addition to species ranging up from the Svenskeegga Member, *Streblopteria* cf. *eichwaldi*, *Streblopteria* ? sp. and *Palaeolima nakamurai* appear from the lower part, but they have not been found from the upper part. The upper part is relatively rich in bivalve fossils. *Grammatodon* (*Cosmetodon*) ? *suzukii*, *G. (C.)* ? sp., *Etheripecten keyserlingi*-formis, *E. aff. sichuanensis*, *E.?* *alatus*, *Streblochondria winsnesi* and *Cassianoides sexcostatus* appear here.

The intimate relationship of the Spitsbergen fauna with that of the Russian Arctic region (Ural, Pechora, Russian Platform, Verkhoyansk) is shown by the occurrence of the following species:

| | Vöringen | Svenkeegga Member | Hovtinden Member | |
|--|----------|-------------------|------------------|-------|
| | | | Lower | Upper |
| 1. <i>Grammatodon</i> (<i>Cosmetodon</i>)? <i>suzukii</i> sp. nov. | | | | * |
| 2. <i>Grammatodon</i> (<i>Cosmetodon</i>)? sp. ind. | | | | * |
| 3. <i>Acanthopecten licharewi</i> (Fredericks) | | X | ★ | * |
| 4. <i>Etheripecten keyserlingiformis</i> (Licharew) | | | | * |
| 5. <i>Etheripecten</i> cf. <i>mutabilis</i> (Licharew) | | ☆ | ★★ | ★★☆ |
| 6. <i>Etheripecten</i> aff. <i>sichuanensis</i> (Chen et al.) | | | | * |
| 7. <i>Etheripecten wilczeki</i> (Toula) | | * | | ★☆ |
| 8. <i>Etheripecten</i> ? cf. <i>alatus</i> (Lyutkevich and Lobanova) | | | | |
| 9. <i>Vorkutopecten svalbardensis</i> sp. nov. | ★ | ★ | ★★★ | ★★★ |
| 10. <i>Vorkutopecten</i> aff. <i>svalbardensis</i> sp. nov. | ★ | | | |
| 11. <i>Cassianoides sexcostatus</i> (Stuckenbergl) | | | | * |
| 12. <i>Streblochondria winsnesi</i> sp. nov. | | | | ★★ |
| 13. <i>Deltopecten</i> sp. ind. | | ★ | ☆ | |
| 14. <i>Streblopteria</i> cf. <i>eichwaldi</i> (Stuckenbergl) | | | ★ | |
| 15. <i>Streblopteria</i> ? sp. ind. | | | ★ | |
| 16. <i>Palaeolima nakamurai</i> sp. nov. | | | * | |

Figure 3. Compiled range-chart of bivalve fossils. *: Festningen, ☆: Reinodden, ★: Ahlstrandodden, ×: Skansbukta.

Acanthopecten licharewi (Asselian–Artinskian of the Urals, Kungurian of Pechora, Lower Permian of Verkhoysansk), *Etheripecten keyserlingiformis* (Upper Carboniferous?–Lower Permian of the Urals and Pechora), *E. cf. mutabilis* (Upper Carboniferous–Lower Permian of the Urals, Timan, Siberia), *E.? alatus* (Lower Permian of Pai Khoi in Siberia), *Streblopteria* cf. *eichwaldi* (Artinskian of the Urals and Russian Platform), and *Cassianoides sexcostatus* (Artinskian of the Urals and Russian Platform). *Cassianoides sexcostatus* is also reported from the Guadalupian of the United States (Branson, 1930; Ciriacks, 1963) and *Etheripecten sichuanensis* occurs in the Upper Permian of South China (Cheng et al., 1974).

The stratigraphic occurrences of these species suggest that the Kapp Starostin Formation ranges in age from Artinskian to Kungurian. This is somewhat earlier than the age range inferred from the brachiopods and bryozoans, but the materials are poor and the conclusion is not definitive.

The Kapp Starostin Formation is conformably overlain by the Lower Triassic Vardebukta Formation of the Sassendalen Group (Nakazawa et al., 1990; Nakamura et al., 1990). The earliest Triassic age of the basal part of this formation is indicated by the occurrence of *Otoceras boreale* Spath together with *Claraia stachei* (Bittner) (Kortshinskaya, 1986; Nakazawa et al., 1987). Hence, a time-gap corresponding at least to Dzhulfian–Dorashamian ages is indicated between the Permian and the Triassic beds.

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Systematic description

Order Arcoida Stoliczka, 1871
Family Parallelodontidae Dall, 1890
Subfamily Grammatodontinae Branson, 1942
Genus *Grammatodon* Meek and Hayden, 1861
Subgenus *Cosmetodon* Branson, 1942

Grammatodon (*Cosmetodon*)? *suzukii* sp. nov.

Figures 4–1a, b

Parallelodon sp. ind. Frebold, 1937, p. 55, pl. 1, figs. 8, 9.

Materials.—A pair of left and right external molds.

Holotype, Reg. no. HP 100050.

Etymology.—Dedicated to Dr. Hiroyuki Suzuki of Doshisha University, who worked in the field with the author.

Diagnosis.—Permian *Grammatodon* characterized by well developed, fine radial ribs and a little arcuate ventral margin.

Description.—Shell moderate in size, a little inflated, elongated subquadrate with subparallel dorsal and ventral margins, rounded anterior and truncated posterior margins; ventral margin slightly arcuate; 41 mm long and 19 mm high; umbo broad and low, raised above the hinge margin, situated at anterior one-fifth of shell length; bluntly rounded umbonal ridge running from the umbo to the posteroventral extremity; surface covered by numerous, weak radial striae, wider than the interstices, approximately fifteen per centimetre width on the medial surface of the shell, one centimetre from the umbo; densely spaced concentric growth lines form cancel-late sculpture with the radials (Figure 4-1b); hinge and internal characters not observable.

Comparison.—Two incomplete specimens illustrated by Frebold (1937) from near the same horizon at Festung (= Festningen) are identical with the present species. Based on Permian material from Malaysia, Yancey (1985) pointed out the possibility that most of the Paleozoic species described as *Parallelodon* should be referred to *Grammatodon* (*Cosmetodon*). Although the present species does not show its hinge characters, it is identified with that genus on the basis of its external shape and ornament. It is similar to the Guadalupian *Cosmetodon multistriatus* (Girty, 1908, p. 423, pl. 31, figs. 13, 14) in its shape and weak radial ornament, but it differs from that species in having less numerous radial striae, a little arcuate ventral margin and a larger size.

Occurrence.—Rare in black shale of the uppermost fossil horizon, in the Hovtinden Member (F11) at Festningen.

***Grammatodon* (*Cosmetodon*)? sp. ind.**

Figures 4-2a, b

Genus (*Parallelodon*)? et sp. ind. Frebold, 1937, p. 56, pl. 2, fig. 4.

Material.—One incomplete, right external cast. Reg. no. HP 100051.

Description.—Posterodorsal marginal part is missing. Preserved part of the specimen is 30 mm long and 18.5 mm high. It is twice as long as high judging from the growth line. Surface is covered by numerous, close-set radial striae and

growth lines which are very weak, but visible under the magnifying glass. The radials reach about forty per centimetre width on the medial part of the shell, one centimetre from the umbo (Figure 4-2b).

Discussion.—The present material most probably belongs to the species doubtfully referred to *Parallelodon* by Frebold (1937) from Festningen. It is similar to *G. (C.)? suzukii* in shape, but differs from it in more densely spaced and more irregular radial ornament. In its numerous radial striae it is similar to *Grammatodon multistriatus* (Girty), but it has a different shape with a more convex ventral margin than the latter species. Evidence is not adequate to support a new species for this specimen.

Occurrence.—Locality and horizon are identical with those for the preceding species.

Order Pterioidea Newell, 1965

Superfamily Pectinacea Rafinesque, 1815

Family Aviculopectinidae Meek and Hayden, 1864

Subfamily Aviculopectininae Meek and Hayden, 1864

Genus ***Acanthopecten*** Girty, 1903

Acanthopecten licharewi (Fredericks, 1915)

Figures 4-3—5

Pterinopecten Licharewi Fredericks, 1915, p. 28, pl. 1, fig. 14.

Aviculopecten (*Acanthopecten*?) *licharewi* (Fredericks). Licharew, 1927, p. 91, pl. 6, fig. 24.

Acanthopecten licharewi (Fredericks). Muromtseva, 1984, p. 66, pl. 25, fig. 26; pl. 28, figs. 7, 8, 11, 12.

Materials.—One nearly complete and one incomplete external cast of left valves, an incomplete external mold of a left? valve, and an incomplete external mold of a right valve. Reg. nos. HP 100052~55.

Description.—All the specimens are incomplete internal molds or somewhat abraded external casts, and the details of the ornament are imperfectly preserved.

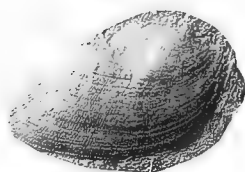
Shell small, subequivalve, subcircular in shape; left valve a little inflated; right valve nearly flat; anterior auricle of left valve trigonal and sharply defined; posterior auricle relatively large, flat, alate and protruding posterodorsally, but not sharply defined from the disc. Shape variable, probably due to secondary deformation; one left valve of nearly equal height and length, with an apical angle of 100° (Figure 4-3) and another left valve more elongate (L/H ratio of 1.34) with

Table 1. Measurements of *Acanthopecten licharewi* (Fredericks). Abbreviations and notation of Tables 1-8. L: length, H: height, U: distance of umbo from the anterior end of the shell, l: hinge length, r: total number of radial ribs, $r_{1,2}$: number of primary and secondary radials, respectively, r_{2-4} : number of secondary to fourth-order radials between primary radials, r_{3+4} : number of third- and fourth-order radials between primary and secondary radials, c: number of comarginal lamellae or costae, a: apical angle (in degrees), V: valve (R: right, L: left), *: estimated value, linear dimensions in mm, Hor.: horizon.

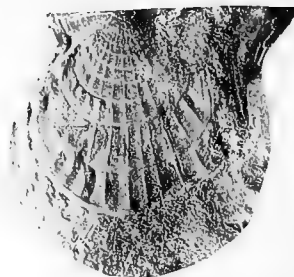
| Reg. | no. | L | H | H/L | a | r | c | V | Hor. |
|------|--------|-------------------|-----------------|------|-----|-----------------|----------------|---|------|
| HP | 100052 | 23.0 | 19.5* | 0.85 | 100 | 13 | 11 | L | AP 6 |
| HP | 100055 | 20.5 ₊ | — | — | 120 | 17 | 9 ₊ | R | AP 6 |
| HP | 100054 | 28.5 | 22 ₊ | — | — | 14 ₊ | 6 ₊ | R | AP 6 |
| HP | 100053 | 14 ₊ | 14.8 | — | — | 8 ₊ | 7 | L | SA 7 |



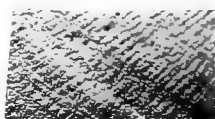
1a



2a



3



2b



1b



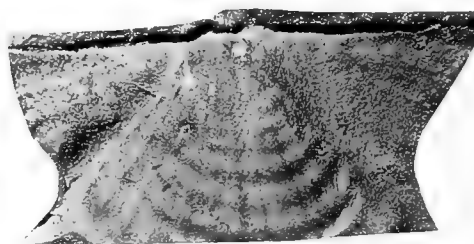
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4



6



7b



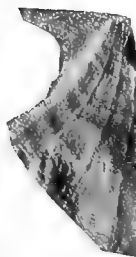
7a



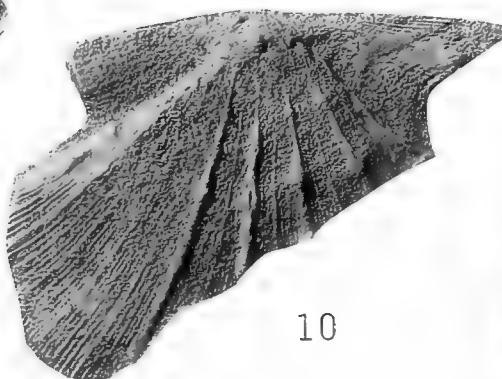
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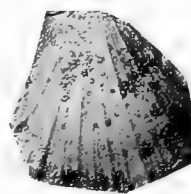
11



9



10



12

a larger apical angle, 120° ; radial ribs narrow and widely spaced varying in number from 13 to 17; interspaces between radials slightly concave or nearly flat; lamellose comarginal sculpture widely disposed, becoming wider later in growth stage with distally oriented spines in the middle of the interspaces of the radial ribs (Figure 4–5).

Discussion.—This species is similar to the Lower Permian *Acanthopecten licharewi* (Fredericks, 1915) from the Urals, Pechora and Verkhoyansk, and to the Upper Carboniferous *Acanthopecten carbonarius* (Stevens) reported from the United States (e.g., Newell, 1938), China (Chao, 1927), and the Donetz Basin (Jakowlew, 1903) in its small size and relatively small number of radial ribs. According to Muromtseva (1984), *A. licharewi* is distinguished from *A. carbonarius* in having less numerous radial ribs and completely flat interspaces between the radials. In these respects, the present material is identical with *A. licharewi*.

Occurrence.—Rare in calcareous shale or muddy siliceous limestone of Unit 5 (lower part of Hovtinden Member) at Ahlstrandodden (AP 6), and in black shale of Unit 7 (upper part of Svenskeegga Member) at Skansbukta (SA 7). According to Thore S. Winsnes (personal communication, 1995) it also occurs in Permian strata in the valley north of Stensiöfjellet, inner Sassendalen.

Subfamily Etheripectininae Waterhouse, 1982

Genus *Etheripecten* Waterhouse, 1963

Discussion.—This genus was introduced by Waterhouse (1963) based on *Etheripecten striatura* Waterhouse from the Upper Permian of New Zealand. The ornament of the left valve resembles that of "*Aviculopecten*" with radial ribs increasing in number by insertion and differentiated into more than two orders. The radial ribs of the right valve of this species also increase in number by insertion, but are usually weaker and less differentiated than those of the left valve. In "*Aviculopecten*", the number of radial ribs of the right valve increases by bifurcation or ramification. In this respect, *Etheripecten* is similar to *Limipecten*, but according to Waterhouse (1969) the concentric lamellae between radial ribs of *Etheripecten* point dorsally, while those of *Limipecten* point ventrally as in the case of *Aviculopecten planoradiatus* McCoy, the type species. Recently, Newell and Boyd (1995) reexamined the Late Paleozoic pectinoids. They defined *Aviculopecten* and Aviculopectinidae as bivalves with equiconvex shells, provided with simple plicae in both valves. On the other hand, the family Etheripectinidae is characterized by inequiconvex and paradiscordant shells, with multi-

costate ornament. Newell and Boyd stressed the variability of multiplicated ribbing and concentric sculpture in this family, treating the genera *Aviculopecten* and *Deltopecten* of authors, *Etheripecten* Waterhouse, *Paradoxipecten* Zhang, *Corrugopecten* Waterhouse, *Fletcheripecten* Waterhouse and *Squamuliferipecten* Waterhouse as synonyms of *Heteropecten* Kegel and Costa. In this case, *Heteropecten* contains a vast number of species with various kinds of ornamentation. In this paper, *Etheripecten* is treated as a distinct genus from *Heteropecten*, the type species of which, *Aviculopecten catharinae* Reed, has broad and bifurcated radial ribs in the right valve. *Fletcheripecten* and *Paradoxipecten* are here considered to be synonyms of *Etheripecten*.

Etheripecten keyserlingiformis (Licharew, 1927)

Figures 4–6, 7a, b

Pecten (*Aequipecten*) ? *keyserlingiformis* Licharew, 1927, p. 33, pl. 3, figs. 1–3; Frebold, 1937, p. 52, pl. 7, fig. 7.

Aviculopecten keyserlingiformis (Licharew). Muromtseva, 1984, p. 60, pl. 28, fig. 10.

Materials.—One nearly complete, left semiexternal cast (HP 100056) and one incomplete, left internal mold (HP 100057).

Description.—Shell medium in size, pectiniform, a little inflated, prosocline, extended posteroventrally; disc fan-like in shape with slightly arcuate anterodorsal, nearly straight posterodorsal, and rounded ventral margins; anterior auricle trigonal with slightly convex anterior margin; posterior auricle a little larger than anterior one, sinuated posteriorly; hinge margin straight, shorter than shell length; ligament area narrow, nearly smooth, provided with a trigonal alivincular ligament pit beneath the umbo (Figure 4–7b); umbo not prominent, slightly salient above the hinge margin, situated at about anterior two-fifths of shell length; surface ornamented with nine or ten slender primary radial ribs alternating with secondaries, some of which become as strong as the primaries; two or three radial riblets of third and fourth order inserted in each interspace; strong concentric folds developed over the whole surface of the disc, more widely spaced in later growth stage; three radial ribs observable on anterior auricle, and obsolete ones on posterior auricle.

Discussion.—These specimens are identical with *Pecten* (*Aequipecten*) *keyserlingiformis* reported by Licharew (1927) and Frebold (1937), in its characteristic ornamentation. Probably due to secondary deformation, one specimen (Fig-

Figure 4. 1a, b. *Grammatodon* (*Cosmetodon*) ? *suzukii* sp. nov., 1a: a pair of external molds of left and right valves, holotype (HP 100050), 1b: enlarged figure showing details of sculpture, $\times 2.5$. 2a, b. *Grammatodon* (*Cosmetodon*) ? sp., 2a: right external cast (HP 100051), 2b: enlarged figure showing details of sculpture, $\times 4$. 3–5. *Acanthopecten licharewi* (Fredericks), 3, 4: left semiexternal casts (HP 100052 and 53), $\times 2$ and $\times 1.5$, 5: right external mold (HP 100054), $\times 1.5$. 6, 7a, b. *Etheripecten keyserlingiformis* (Licharew), 6: left semiexternal cast (HP 100056), 7a: left semiexternal cast (HP 100057), 7b: enlarged figure showing alivincular ligament pit (arrow), $\times 2.5$. 8, 9. *Etheripecten wilczeki* (Toula), 8: gypsum cast of left external mold (HP 100058), $\times 1.5$, 9: left external mold (HP 100059), $\times 2$. 10. *Etheripecten* sp. aff. *E. sichuanensis* (Chen *et al.*), gypsum cast of left external mold (HP 100060). 11, 12. *Etheripecten* sp. cf. *E. mutabilis* (Licharew), 11: gypsum cast of left external mold (HP 100062), 12: left semiexternal cast (HP 100071). All are in natural size unless otherwise indicated.

Table 2. Measurements of *Etheripecten keyserlingiformis* (Licharew).

| Reg. | no. | L | H | H/L | r ₁₊₂ | r ₃₊₄ | a | c | Hor. |
|------|--------|------|------|------|------------------|------------------|-----|----|------|
| HP | 100056 | 45.5 | 40.0 | 0.89 | 18 | 3 | 115 | 15 | F 11 |
| HP | 100057 | — | 17.6 | — | 15 ₊ | 1~2 | 90 | 11 | F 11 |

ure 4-6) is extended posteroventrally and has a more elongated shape than the previously described species, but another (Figure 4-7a) has a shape and ornamentation similar to the type specimen. Although the right valve of this species has not been reported, the shape and ornamentation of its left valve are very similar to those of *Etheripecten striatura* Waterhouse, the type species of the genus, so the species is here included in *Etheripecten*.

Occurrence.—Rare in black shale of the uppermost fossil horizon of the Hovtinden Member at Festningen (F11).

***Etheripecten wilczeki* (Toula, 1875)**

Figures 4-8, 9

Pecten (*Aviculopecten*) *Wilczeki* Toula, 1875a, p. 152, pl. 1, fig. 12.
Pecten wilczeki Toula. Frebold, 1937, p. 54.

Materials.—One nearly complete, left external mold and several fragmental molds of left valves. Reg. nos. HP 100058, 59.

Description.—Shell relatively small, pectiniform, a little inflated; fan-like in shape, with nearly straight anterodorsal, slightly dorsally arcuate posterodorsal, and rounded ventral margins; prosocline, extended posteroventrally; umbo not prominent, slightly salient above the hinge margin, lying at about anterior two-fifths of shell length; apical angle 95–110°; anterior auricle small, trigonal; posterior auricle a little larger than the posterior one, alate with arcuate posterior margin; both auricles sharply distinct from disc; surface of the shell ornamented with nine primary radial ribs; wide, nearly flat interspaces are sculptured by 8–12 weak, radial threads, some a little stronger than the rest referred to as secondary ribs, but not alternating with the primaries; umbonal part of the shell, to 16 mm, ornamented with concentric wrinkles, which later fade away; two or three radial striae discernible on both auricles; ligament unknown.

Comparison.—The type specimen described by Toula has seven strong, slender radial ribs, and smooth interspaces without finer radial ribs. *Pecten* (*Aequipecten*) ? *wilczekiformis* Licharew (1927, p. 35, pl. 3, figs. 4, 6, 7) is distinguished from *E. wilczeki* in its development of interstitial radial riblets.

According to Frebold (1937) the type specimen of *E. wilczeki* is not well preserved. He recognized the presence of finer radial ribs in the marginal area of his specimen, where the shell is preserved, and regarded the two species as being conspecific. However, the finer interstitial radial ribs of the specimen described here are very weak, numerous and subequal in strength, whereas those of *P.(A.) ? wilczekiformis* are differentiated into second, third or even fourth orders. Both species are considered to belong to *Etheripecten*. *E. wilczekiformis* is more closely allied to *E. keyserlingiformis* than to *E. wilczeki*. *E. wilczeki* is most similar to *Euchondria cancellata* Gu and Liu (1976, p. 171, pl. 12,

figs. 17, 18), from the Lower Permian Kufeng Series of South China, in shape and ornament. It differs only a little from the latter species in its lesser development of concentric folds and greater height relative to length. The genus *Euchondria* is characterized by a costate left valve, a nearly smooth right valve, and a series of ligament pits perpendicular to the hinge margin, in addition to a large, central ligament pit. In *E. cancellata* only left valves are known and the hinge character is unknown. Therefore, its generic position is uncertain.

Occurrence.—Rare in calcareous shale of the uppermost horizon of the Svenskeegga Member at Festningen (F5); rare in muddy limestone of the upper part of the Hovtinden Member at Ahlstrandodden (AP 7, 8) and Reinodden (RP 9).

Etheripecten* sp. aff. *E. sichuanensis

Chen, Zhang and Xu, 1974

Figures 4-10

Resembles.—

Etheripecten sichuanensis Chen, Zhang and Xu, 1974, p. 302, pl. 158, figs. 14, 17; Fang, 1987, p. 373, pl. 2, figs. 1-6.

? *Etheripecten sichuanensis* Liu, 1976, p. 179, pl. 13, figs. 10-13; Gan and Yin, 1978, p. 336, pl. 14, figs. 17, 20.

Etheripecten hunanensis Zhang, 1981, p. 261, pl. 2, figs. 6-8.

Material.—One incomplete left external mold obtained by dissolving away shell material. Reg. no. HP 100060.

Description.—Shell relatively large, a little inflated, longer than high, estimated to be 65 mm long and 58 mm high; disc fan-like in shape with straight antero- and posterodorsal margins and a broadly rounded ventral margin; hinge margin straight, a little shorter than shell length; anterior auricle small, subtrigonal, a little inflated, clearly separated from the disc by a sulcus; posterior auricle large, flat, sinuated posteriorly, protruding posterodorsally; umbo subdued, slightly salient above hinge margin; apical angle 110°; surface ornamented with radial ribs of three orders; primaries seven in number, strong and round-topped, alternating with weaker secondaries; five to six, thread-like radial riblets of third order inserted in each interspace; auricles with radial and concentric sculpture making a lattice ornament; hinge not preserved.

Discussion.—The external shape and the ornamentation indicate a close relationship of this species with *Etheripecten sichuanensis* Chen, Zhang and Xu (1974) and *E. hunanensis* Zhang (1981), both from the Upper Permian Luntang Series in South China. The former species was later illustrated as ? *E. sichuanensis* sp. nov. by Liu (1976) based on the same specimens. Zhang distinguished *E. hunanensis* from *E. sichuanensis* by the presence of striations and spinose projections on the primary ribs. According to Fang (1987), however, these differences represent infraspecific variation.

The specimen described here differs from *sichuanensis* in its more elongate shape with larger apical angle and larger size.

Occurrence.—Arenaceous limestone of the upper part of the Hovtinden Member at Festningen (F8).

***Etheripecten* sp. cf. *E. mutabilis* (Licharew, 1927)**

Figures 4–11, 12; Figures 5–1—4

Pecten (*Aequipecten*) *Kokscharofi* Toulou (non Verneuil), 1873, p. 20, pl. 5, fig. 6.

Aviculopecten cf. *hiemalis* Salter. Licharew, 1927, p. 76, pl. 5, figs. 18–21; pl. 6, fig. 1.

? *Aviculopecten* (*Dellopecten*) cf. *mutabilis* Licharew and A. cf. *hiemalis* Salter. Frebold, 1937, p. 51, pl. 1, figs. 2, 3.

Compared with.—

Pecten (*Aequipecten*) *Bouei* Toulou, 1873, p. 19, pl. 5, fig. 8.

Aviculopecten mutabilis Licharew, 1927, p. 72, pl. 5, figs. 7–10, 12, 14–17.

Aviculopecten (*Dellopecten*)? *mutabilis* Licharew. Lyutkevich and Lobanova, 1960, p. 102, pl. 15, figs. 1–6.

Material.—Eight incomplete left valves, one complete and two incomplete right valves. Reg. nos. HP 100061–68, 100070, 71.

Description.—Shell moderate in size, inequivalve, inequilateral, prosocline, nearly as long as high, apical angle 90–100°. Left valve moderately inflated; umbo not prominent, a little salient above the hinge margin; beak situated at about anterior one-third of shell length; disc fan-like in shape with slightly concave anterodorsal, nearly straight posterodorsal, and well rounded ventral margins; anterior auricle subtriangular, with a rounded anterior margin, demarcated from the disc by a sulcus; posterior auricle only partly preserved; surface covered with many radial ribs differentiated into three or four orders; primary ribs 7 to 9 in number, strong, round-topped, a little projected at ventral margin; second- and third- order radials alternating regularly with lower-order radials; some tertiary radials as strong as secondaries; fourth-order radials very weak, sporadically inserted near the margin; growth lines close-set, curving ventrally on radial ribs and dorsally on interspaces, showing scaly or spinose projections on the primary ribs (Figures 5–1b, 2). Right valve nearly flat; anterior auricle deeply incised below; posterior auricle subtriangular, nearly equal in length to the anterior auricle, a little sinuated posteriorly; numerous radial ribs increasing in number by insertion; first- and second-order radials becoming subequal in strength; a

small number of third-order radials, very weak and thread-like; total number of radials, 34; close-set, weak concentric sculpture, making a lattice ornament with the radials; alivincular ligament pit partly seen in one left internal mold.

Remarks and comparison.—In this material, the number of radial ribs increases by insertion in both the left and right valves. The comarginal sculpture curves ventrally on the radial ribs and dorsally on the interspaces. Therefore, these specimens are referred to *Etheripecten* Waterhouse (1969). In their well differentiated radial ornament and robust primary radial ribs, these shells are identical with *Pecten* (*Aequipecten*) *kokscharofi* as described by Toulou (1873), *Aviculopecten* cf. *hiemalis* Licharew (1927), and probably *Aviculopecten* (*Dellopecten*) cf. *mutabilis* and A. (*D.*) cf. *hiemalis* Frebold (1937). They are very similar to *Aviculopecten mutabilis* Licharew (1927). According to Licharew (1927) the latter species is distinguished from *Aviculopecten* cf. *hiemalis* by its more pointed posterior auricle, the sharper restriction of auricles from the disc, the weaker bend of antero- and posterodorsal margins of the disc, and less regularity in the appearance of ribs. These differences, though, are not distinctive, as noted by Licharew himself. A. cf. *hiemalis* of Licharew has generally more robust primary radials than *A. mutabilis*. It is clearly distinguished from the original *A. hiemalis* reported from the Himalayas (cf. Diener, 1897, p. 9, pl. 5, figs. 10a, b, 11) in taller shape and smaller posterior auricle and is more closely related to *A. mutabilis*. Lyutkevich and Lobanova (1960) illustrated the right valve of *A. mutabilis* (pl. 15, figs. 2, 5), which shows inserted radial ribs. Therefore, *A. mutabilis* is considered to belong to the genus *Etheripecten*. The right valve of *Etheripecten mutabilis* has less uniform radial ornament than the present species.

Occurrence.—Common in the Hovtinden Member at Festningen, Reinodden, and Ahlstrandodden; rare in Svenskeegga Member at Reinodden.

Etheripecten* ? sp. cf. *E. alatus

(Lyutkevich and Lobanova, 1960)

Figures 5–5

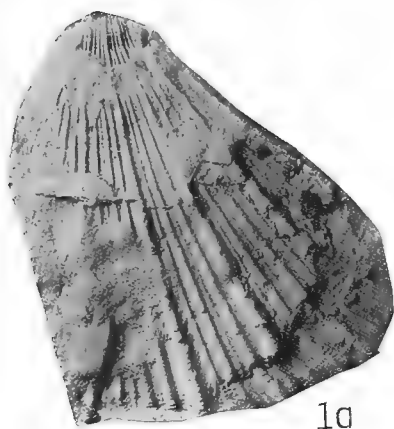
Compared with.—

Pseudomonotis alata Lyutkevich and Lobanova, 1960, p. 116, pl. 17, fig. 9.

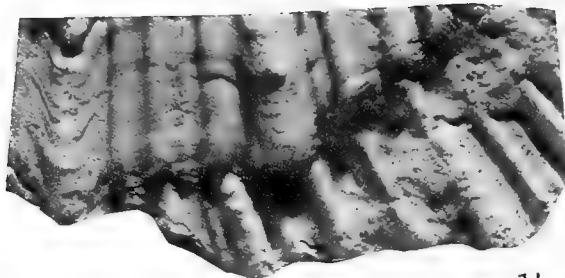
Description.—Only one incomplete, semiexternal cast of a

Table 3. Measurements of *Etheripecten* sp. cf. *E. mutabilis* (Licharew). ☆ : Total number of primary and secondary radial ribs, #: total number of radial ribs.

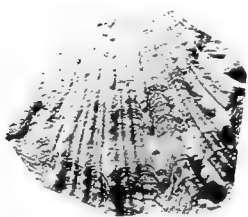
| Reg. | no. | L | H | H/L | U | U/L | r ₁ | r _{2–4} | a | V | Hor. |
|------|--------|-----------------|-----------------|------|------|------|----------------|------------------|-----|---|------|
| HP | 100060 | 60 ₊ | 58 ₊ | — | — | — | 7 ₊ | 4~6 | 100 | L | F 9 |
| HP | 100062 | 21.5 | 22.8 | 1.06 | — | — | 7 | 3 | 85 | L | RP 3 |
| HP | 100063 | 22.3 | 21.5 | 0.96 | 8.0 | 0.36 | 26☆ | — | 90 | R | F 11 |
| HP | 100064 | 30 ₊ | 32 ₊ | — | — | — | 6 ₊ | 3~4 | — | L | F 9 |
| HP | 100065 | 33.5 | 35.0 | 1.04 | 12.5 | 0.37 | 9 | 3~5 | 90 | L | F 11 |
| HP | 100066 | 21.0 | — | — | — | — | 24# | — | 85 | R | F 11 |
| HP | 100067 | 25.0 | 25.0 | 1.00 | 7.5 | 0.30 | 8 | 3~4 | 90 | L | F 11 |
| HP | 100071 | 25.3 | 25.7 | 1.02 | 10.5 | 0.42 | 7 | 3 | 90 | L | F 7p |



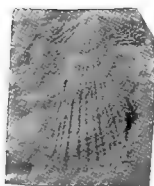
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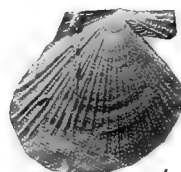
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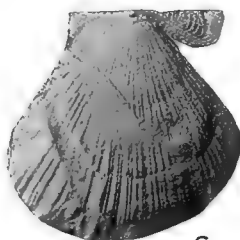
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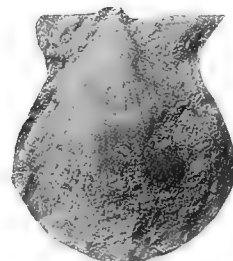
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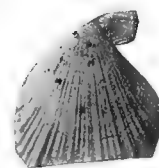
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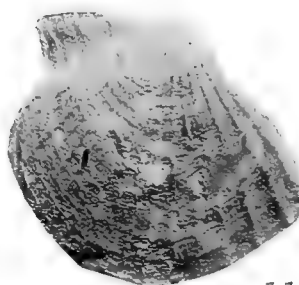
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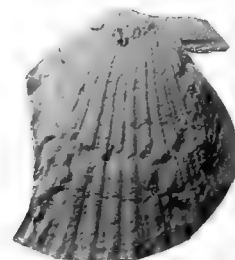
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11



12

left? valve is available (Reg. no. HP 100069). More than posterior one-third of the shell is not preserved. Shell 38 mm high and more than 30 mm long, nearly flat; disc inferred to be fan-like in shape; anterodorsal margin straight; anterior auricle trigonal, flat, clearly marked off from the disc; surface ornamented with six strong, round-topped primary radial ribs; broad, flat or slightly concave interspaces with weak secondary and tertiary radials five to eight in number; close-set weak concentric striae partly preserved.

Discussion.—The present material is quite similar in shape and sculpture to *Pseudomonotis alata*, described on the basis of a right valve by Lyutkevich and Lobanova (1960) from the Lower Permian at Pai Khoi of the northern coast of Siberia. It differs slightly from that species in taller outline. The well differentiated, straight radial ornament of these Siberian and Spitsbergen species suggests that they belong to *Etheripecten* rather than to *Pseudomonotis*.

Occurrence.—Dark grey calcareous shale of Unit G of the Hovtinden Member at Reinodden (RP 9).

Family Streblochondriidae Newell, 1938

Genus *Streblochondria* Newell, 1938

***Streblochondria winsnesi* sp. nov.**

Figures 6–2a, b–4

Pecten (*Pseudamusium*) cf. *ufaensis* Tschernyschew. Frebold, 1937, p. 53, pl. 1, fig. 3–5.

Material.—One complete right valve (external and internal molds, holotype, Reg. no. HP 100094a, b) and a nearly complete right valve (internal and external molds, Reg. no. HP 100095a, b). Holotype specimen occurs in black shale of Unit 11 of the Hovtinden Member at Festningen.

Etymology.—Dedicated to Thore S. Winsnes for his contribution to the geological understanding of West Spitsbergen.

Diagnosis.—Permian *Streblochondria* characterized by a broad shape and very fine cancellate ornament composed of numerous radial and concentric striae.

Description.—Shell medium in size, a little inflated, and subcircular in shape, with well rounded ventral, slightly convex posterodorsal, and slightly concave anterodorsal margins; as long as high; opisthocline; umbo subdued, not salient above the hinge margin; apical angle varying from 90° to 110°; posterior auricle very small, obtuse-triangular, truncated posteriorly; anterior auricle relatively large, rounded trigonal, and marked below by deep slit-like byssal notch; surface covered with numerous, uniform radial striae increasing in number by insertion, 70 per cm in the medial area 1 cm away from the umbo; dense concentric fila

Table 4. Measurements of *Streblochondria winsnesi* sp. nov.

| Reg. | no. | L | H | H/L | I | a | Hor. |
|------|--------|------|------|------|-----|--------|------|
| HP | 100094 | 33.5 | ca33 | 0.99 | 9.5 | 90~110 | F 11 |
| HP | 100095 | 20.0 | 20.0 | 1.00 | — | 90~110 | AP 9 |

making a cancellate ornament with the radials, slightly raised scales on the radials; anterior auricle ornamented with five distinct radial ribs and growth lines; hinge characters unknown.

Discussion.—Frebold (1937) illustrated three right valves identified as *Pecten* (*Pseudamusium*) cf. *ufaensis* Tschernyschew from the upper part of the Kapp Starostin Formation at Festningen. One of them shows a distinct sculpture, very similar to that described here, so it is considered to be conspecific with this species. It is similar to *Streblochondria sculptilis* (Muller), the type of the genus, from the Carboniferous of the United States (cf. Newell, 1938, p. 38, pl. 16, figs. 5a–c, 7, 9a, b). However, the present new species has a larger apical angle, a lower outline, and finer ornament than that species. It is more closely allied to *S. ufaensis* (Tschernyschew) (Licharew, 1927, p. 30, pl. 2, figs. 7, 8; Lyutkevich and Lobanova, 1960, p. 131, pl. 21, fig. 1), but differs from that species in the finer radial sculpture as noticed by Frebold and, furthermore, in its longer outline.

Occurrence.—Rare in siliceous limestone of the upper part of the Hovtinden Member at Ahlstrandodden (AP 9), and the uppermost horizon of the Hovtinden Member at Festningen (F11).

Genus *Streblopteria* M'Coy, 1851

Streblopteria* sp. cf. *S. eichwaldi
(Stuckenberg, 1898)

Figures 6–6, 7a, b, c

Pecten (*Aviculopecten*) cf. *ellipticus* Toulou, 1873, p. 20, pl. 5, fig. 1.
Pecten (*Pseudamusium*) sp. ind. ex aff. *sericeus* Frebold, 1937, p. 54.

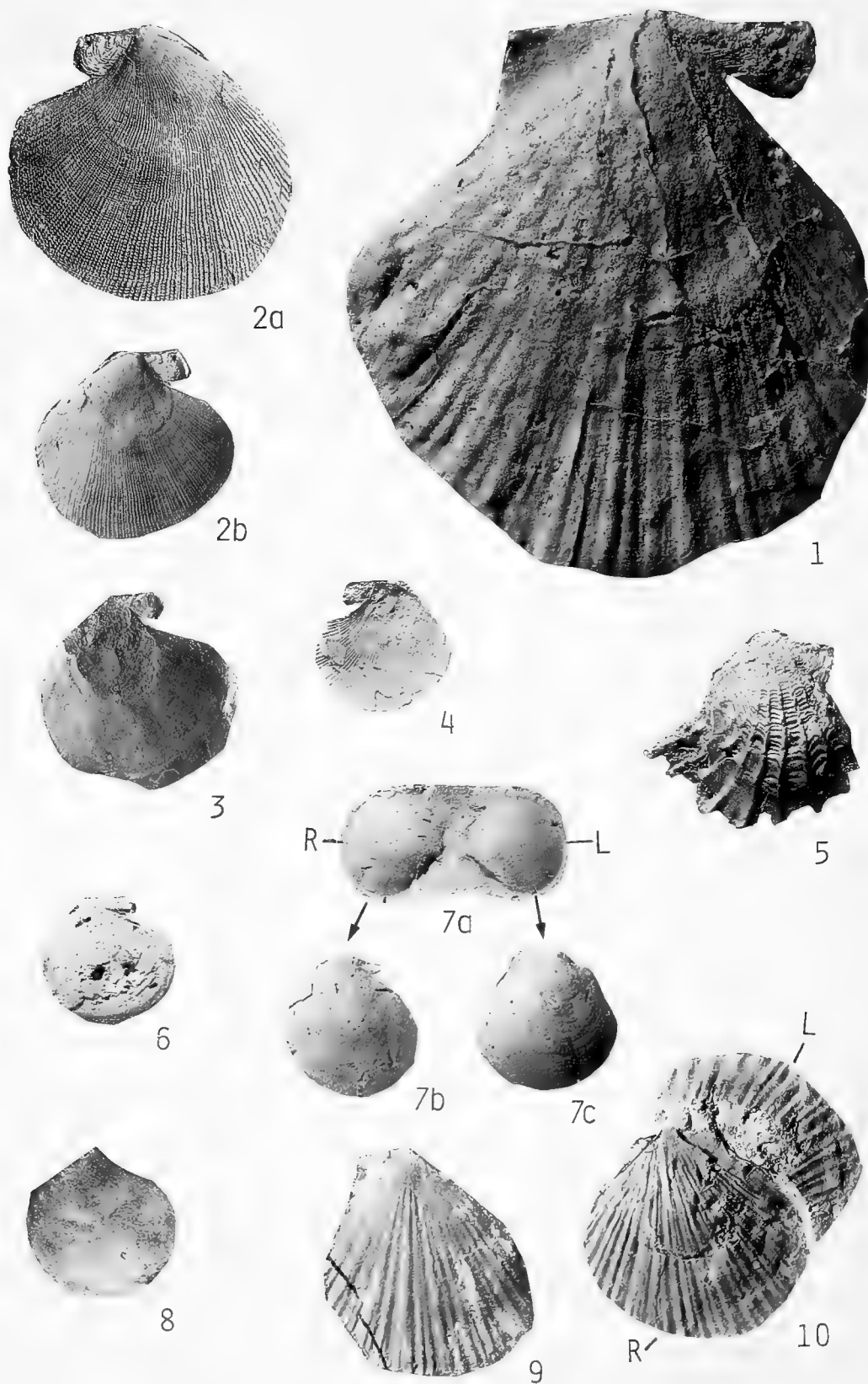
Compared with.—

Pecten Eichwaldianus Stuckenberg, 1898, p. 203, pl. 1, figs. 25a, b.

Materials.—A pair of valves, two internal molds, and two incomplete external molds. Reg. nos. HP 100087~90.

Description.—Shell small, nearly equivalve, subcircular in shape, opisthocline, a little extended anteriorly; left valve gently inflated; right valve slightly less convex than left; anterodorsal margin of the disc a little concave, ventral and posterior margins well rounded; umbo lying a little posterior to the middle of the shell, not salient above the hinge

Figure 5. 1–4. *Etheripecten* sp. cf. *E. mutabilis* (Licharew), 1a: gypsum cast of left external mold (HP 100061), 1b: enlarged figure showing details of sculpture, $\times 3$, 2: gypsum cast of left external mold (HP 100064), 3: silicon rubber cast of right external mold (HP 100066), 4: gypsum cast of right external mold (HP 100063). 5. *Etheripecten* ? sp. cf. *E. alatus* (Lyutkevich and Lobanova), left? semiexternal cast (HP 100069). 6–10. *Vorkutopecten svalbardensis* sp. nov., 6: gypsum cast of right external mold, holotype (HP 100072), 7: semiinternal mold of left valve, paratype (HP 100076), 8: gypsum cast of right external mold (HP 100075) $\times 1.2$, 9: gypsum cast of right external mold (HP 100077), 10: gypsum cast of right external mold (HP 100078), $\times 1.4$. 11, 12. *Dellopecten* sp., 11: semiexternal cast of left valve (HP 100085), $\times 1.1$. 12: silicon rubber cast of external mold of right valve (HP 100086). All are natural size unless otherwise indicated.



margin; apical angle 90° in umbonal portion and 110–120° in later growth stages; posterior auricle small, obtuse-triangular; anterior auricle larger, obtuse-triangular in left valve, and deeply incised below in the right valve; surface almost smooth, weak concentric sculpture discernible in the internal mold and partly preserved external cast; no radial ornament observed.

Discussion and comparison.—The genus *Streblopteria* was established by McCoy (1851). The Carboniferous *Meleagrina laevigata* McCoy from Ireland was designated as type species by Meek and Worthen (1866). The genus is characterized by smooth shells of acline to opisthocline pectinoid form, and is distinguished from *Streblochondria* Newell (1938) which has cancellate sculptures. The posterior auricle of the type species is much larger than the anterior auricle, poorly distinguished from the disc. However, the forms with a small, obtuse-triangular, more or less clearly defined posterior auricle are also included in *Streblopteria* or referred to *Pseudamusium* Verrill by many authors.

According to Cox *et al.* (1969) *Pseudamusium* is a junior synonym of the Cenozoic genus, *Palliolum* Monterosato. Several small *Pseudamusium* species, such as *P. eichwaldi* (Stuckenberg), *P. pusillus* (Schlothheim), and *P. ellipticum* (Phillips), have very weak radial ribs or cancellate ornament on a limited part of the shell. They were doubtfully assigned to *Streblochondria* by Newell (1938). However, they have a longer shape than *Streblochondria* and are more similar to smooth forms of *Streblopteria* or "*Pseudamusium*". This hardly warrants recognition as a different genus. In this paper, all these species are treated as *Streblopteria*, although they differ somewhat from the type species. The species described here is most similar to *S. eichwaldi* (Stuckenberg, 1898) in shape, but the surface ornament is insufficiently known for specific identification. *Pecten* cf. *ellipticus* reported by Toulou (1873) from the south point of Spitsbergen was referred to *Pecten* (*Pseudamusium*) aff. *sericeus* Verneuil by Frebold (1937). However, *P. sericeus* has a more opisthocline shell that is extended more anteriorly. It is probably identical with the present species.

Occurrence.—Siliceous limestone of the lower part of the Hovtinden Member at Ahlstrandodden (AP 6).

Streblopteria? sp. ind.

Figures 6–8

Discussion.—One incomplete right internal mold (Reg. no. HP 100092), estimated at 24 mm long and a little more than 24 mm high, is at hand. The shell is subcircular in outline and provided with a concave anterodorsal margin. The surface is covered by a weak concentric sculpture. The auricular part of the shell is not preserved. It probably belongs to *Streblopteria*, but is too imperfectly preserved to be certain.

Occurrence.—Siliceous shale of the lower part of the Hovtinden Member at Ahlstrandodden (AP 6).

Family Deltopectinidae Dickins, 1957

Genus *Vorkutopecten* Guskov, 1984

Vorkutopecten svalbardensis sp. nov.

Figures 5–6—10

Material.—Eight right external and internal molds and three left external and internal molds. Reg. nos. HP 100072–83 (holotype HP 100072). Holotype from Unit 9 of the Hovtinden Member at Festningen.

Etymology.—Derived from Svalbard Islands, where the species occurs.

Diagnosis.—Shell is higher than long; ornamentation of both left and right valves consists of numerous radial ribs differentiated into three orders, increasing in number by insertion. Concentric costae arch ventrally in the inter-spaces of radial ribs.

Description.—Shell inequivalve, inequilateral, suborbicular in shape, a little higher than long; right valve moderately to weakly inflated; left valve more inflated than right; umbo situated a little anterior to the middle of shell, nearly acline and slightly salient above the hinge margin in the left valve, but not in the right valve; apical angle about 90°; anterior and posterior auricles nearly equal in length; posterior one trigonal and situated posteriorly; right anterior auricle deeply incised below; surface of disc covered with numerous, slender radial ribs narrower than interstices, increasing in

Table 5. Measurements of *Streblopteria* sp. cf. *S. eichwaldi* (Stuckenberg).

| Reg. | no. | L | H | H/L | I | I/L | U | U/L | a | V | Hor. |
|------|---------|-------|------|------|------|------|-----|------|--------|---|------|
| HP | 100087a | 8.0 | 7.5 | 0.94 | 4.0 | 0.50 | 4.0 | 0.50 | ~110 | L | AP 6 |
| HP | 100087b | 8.0 | 7.8 | 0.98 | 3.7* | 0.46 | 4.5 | 0.56 | 90~120 | R | AP 6 |
| HP | 100088 | 12.7 | 11.6 | 0.91 | 5.7 | 0.45 | 7.2 | 0.56 | 90~120 | R | AP 6 |
| HP | 100089 | 13.0* | 12.5 | 0.96 | — | — | 7.5 | 0.57 | ~120 | R | AP 6 |

Figure 6. 1. *Vorkutopecten* sp. aff. *V. svalbardensis* sp. nov., gypsum cast of right external mold (HP100084). 2–4. *Streblochondria winsnesi* sp. nov., 2a: right external mold, holotype (HP 100094), $\times 1.4$, 2b: gypsum cast, 3: right internal mold of the same, 4: right external mold (HP 100095). 5. *Cassianoides sexcostatus* (Stuckenberg), left external mold (HP 100093), $\times 2.4$. 6, 7a–c. *Streblopteria* sp. cf. *S. eichwaldi* (Stuckenberg), 6: right internal mold (HP 100088), $\times 1.5$, 7a: a pair of internal molds of left (L) and right (R) valves (HP 100087), $\times 2$, 7b–c: enlarged figures of right (b) and left (c) valves, $\times 3$. 8. *Streblopteria*? sp., right external cast (HP 100092). 9, 10. *Palaeolima nakamurai* sp. nov., 9: right external cast, paratype (HP 100097), $\times 1.5$, 10: right external cast (R), holotype (HP 100096) and a part of left valve (L), $\times 1.2$. All are natural size unless otherwise indicated.

number by insertion; primary radial ribs varying in number from 12 to 17, with two or three radials of second and third orders in each interspace between the primaries; total number of radials 35 to 50 or more; secondary radials of right valve become as strong as primaries; lamellose concentric sculpture developed on the whole surface, curving dorsally on radial ribs and ventrally in interstices; both auricles sculptured by radial ribs and concentric costae; a small, trigonal ligament pit partly preserved in one left internal mold.

Remarks and comparison.—The radial ribs of both left and right valves increase in number by insertion, as in *Etheripecten*, *Limipecten*, and *Vorkutopecten*. The concentric sculpture swings ventrally between radial ribs as in *Limipecten*, not *Etheripecten*. The shell length of *Limipecten* is usually equal to or larger than the height, and the radial ribs of the right valve are finer and more numerous than those of the left valve. Furthermore, the right valve is nearly flat. The present species has a greater height than length. The ornamentation is similar in both valves, although secondary ribs of the right valve grow as strong as the primaries. The right valve is more or less inflated. In these respects, it can be identified with *Vorkutopecten* established by Guskov (in Muromtseva, 1984), based on *Aviculopecten giganteus talis* Lyutkevich and Lobanova (1960, p. 108, pl. 16, fig. 10; pl. 17, fig. 1). Guskov included two species in the genus in addition to the type species, namely, *Aviculopecten subclathratus* (Keyserling) and *A. netschajewi* Licharew. However, the type specimen of the latter species has branching radial ribs in the right valve and is excluded from *Vorkutopecten*. On the other hand, materials described as *Vorkutopecten netschajewi* by Guskov (Muromtseva, 1984, pl. 29, fig. 8) have inserted radial ribs and cannot be identified with this species, which is more similar to *A. subclathratus*. The Spitsbergen species is similar to *A. subclathratus* and *A. netschajewi* of Guskov, but differs in its more numerous primary radial ribs and larger posterior auricle. *Vorkutopecten*, characterized by broad, alivincular ligament pit and a grooved ligament area, is included in Family Deltopectinidae. The present species has a relatively small ligament pit.

Occurrence.—Common in siliceous limestones of the Hovtinden Member at Festningen (F 7p, F 8 and 9), rare in limestone of the Vøringen Member (AP 1), common in siliceous limestone of the Svenskeegga (AP 2) and the Hovtinden Member (AP 6, 7) at Ahlstrandodden, rare in calcareous sandstone of the Hovtinden Member at Reinodden

(RP 7).

***Vorkutopecten* sp. aff. *V. svalbardensis* sp. nov.**

Figures 6–1

Discussion.—The species is represented by a single, large external mold of a right valve (Reg. no. HP 100084). It is 86 mm long and 91 mm high and has an apical angle of 100°. The shell is gently convex and sculptured with as many as 60 radial ribs. The radials are differentiated into three orders, but due to poor preservation distinction between primary and secondary ribs is difficult. This species is very similar to the preceding new species in shape and ornamentation, but its size is much larger and its apical angle is a little greater.

Occurrence.—Arenaceous limestone of Unit 1 (Vøringen Member) at Ahlstrandodden (AP 1).

Genus *Deltopecten* Etheridge, Jr., 1892

***Deltopecten* sp. ind.**

Figures 5–11, 12

Material.—One incomplete left semiexternal cast, and one incomplete right valve represented by external and internal molds. Reg. nos. HP 100085, 86.

Description.—Shell moderate in size, subcircular in shape, nearly equiconvex and subequilateral; umbo not prominent, located subcentrally; apical angle 100–110°; anterior auricle triangular, with slightly concave anterior margin in the left valve and byssate in the right valve; left posterior auricle not preserved; right posterior one partly preserved, obtuse-triangular and probably smaller than the anterior one; surface of the left valve sculptured by relatively slender, rounded primary ribs, 18 in number, separated by wide interspaces and alternating with very weak, secondary radials; right valve ornamented with flat-topped primary radial ribs; intervening flat interspaces of a width nearly equal to that of the radial ribs, with weak secondary radials inserted in the medial part of the shell; surface of both valves covered with close-set concentric fila swinging slightly ventrally, in the interspaces; ligament not preserved.

Discussion.—Although the ligament cannot be observed, the present species can be referred to *Deltopecten* judging from the nearly equiconvex shell and relatively simple, flat-topped radial ribs. This species is somewhat similar to

Table 6. Measurements of *Vorkutopecten svalbardensis* sp. nov.

| Reg. | no. | L | H | H/L | I | U/L | a | r ₁ | r | V | Hor. |
|------|--------|-------|-------|------|-----------------|------|----|----------------|-----------------|---|------|
| HP | 100072 | 31.0* | 30.5* | 0.98 | 19 ₊ | 0.48 | 88 | 16 | 54 | R | F 9 |
| HP | 100074 | 29.0 | 31.5 | 1.09 | 20.0 | 0.38 | 90 | 11? | 47 | R | F 7p |
| HP | 100075 | 35.0 | 38.0 | 1.09 | 35.0 | 0.46 | 88 | 17 | 46 ₊ | R | F 9 |
| HP | 100076 | 24.0* | 27.0 | 1.13 | — | 0.46 | 85 | 14 | 30 ₊ | L | AP 1 |
| HP | 100077 | 20.0* | 22.0 | 1.10 | — | 0.50 | 90 | 12 | 42 | R | F 7p |
| HP | 100078 | 27.0* | 28.7 | 1.06 | 22.0 | 0.50 | 90 | 12 | 40 | L | AP 1 |
| HP | 100080 | 34.3* | 35.8 | 1.04 | 26.0 | 0.43 | 90 | 12 | 37 | R | AP 2 |
| HP | 100081 | 26.0* | 30.3 | 1.17 | 13.0 | 0.49 | 90 | ? | 35 | R | AP 7 |

Table 7. Measurements of *Deltopecten* sp. ind.

| Reg. | no. | L | H | H/L | U | U/L | a | r ₁ | V | Hor. |
|------|--------|------|------|------|------|------|-----|----------------|---|------|
| HP | 100085 | 35.5 | 33.5 | 0.94 | 16.7 | 0.47 | 105 | 18 | L | RP 7 |
| HP | 100086 | 30+ | 35.0 | — | 17.5 | 0.50 | 110 | 15? | R | AP 2 |

Deltopecten lyonsensis Dickins (1957, p. 41, pl. 7, figs. 1–5 and 9; pl. 8, figs. 11–13; pl. 9, fig. 12; pl. 10, figs. 3–4) from West Australia, but differs from that species in its less numerous primary radial ribs and the development of secondary radials in the left valve.

Occurrence.—Rare in calcareous sandstone of Unit E of the Hovtinden Member at Reinodden (RP 7) and in siliceous limestone of Unit 3 of the Svenskeegga Member at Ahlstrandodden (AP 2).

Family Cassianoididae Newell and Boyd, 1995

Genus **Cassianoides** Newell and Boyd, 1995

Discussion.—The present family and genus were established by Newell and Boyd (1995) on the basis of a single species, *Cassianoides kingorum* Newell and Boyd of the Middle to Late Permian of West Texas. The genus is characterized by small, strongly inequivalve shells; the left valve is strongly convex, ornamented with a few widely spaced, strong primary costae and a few comarginal, tubular hyote spines on the radial ribs; the right valve is flat, sculptured by spineless, subdued radial ribs. *Cyrtostrota sexradiata* Branson (1930, p. 45, pl. 11, figs. 13–15) from the Upper Permian Park City Formation was later shifted to the genus *Cassianella* of the Family Cassianellidae by Ciriacks (1963). This species was considered to be a junior synonym of *Pseudomonotis sexcostatus* Stuckenberg (1898, p. 207, pl. 1, fig. 40) from the Permian of Russia and to belong to *Aviculopecten* by Muromtseva (1984). The species is very similar to *Cassianoides kingorum*, not only in shell form but also in the characteristic ornamentation of both the left and right valves. It undoubtedly belongs to *Cassianoides*.

Aviculopecten crassispinosus Chronic, reported by Newell et al. (1953, p. 155, pl. 33, figs. 10–13) from the Lower Permian of Peru, is also referred to as a member of this genus. *Cassianella rara* described by Waterhouse (1987, p. 145, pl. 3, figs. 1, 7, 10) from the Middle Permian of East Australia is another example. Waterhouse noticed the close relation of this species to *C. sexradiata* and *C. crassispinosus*. His figs. 1 and 7, illustrated as a right valve, are quite similar to the left valve of *A. crassispinosus* (especially fig. 13a of Newell et al., 1953), and are believed to be a left valve. The genus *Crassinoides* is now known from the Permian of the United States, Peru, Australia, Russia, and Spitsbergen.

Cassianoides sexcostatus (Stuckenberg, 1898)

Figure 6–5

Pseudomonotis sexcostatus Stuckenberg, 1898, p. 207, pl. 1, fig. 40.

Cyrtostrota sexradiata Branson, 1930, p. 45, pl. 2, figs. 13–15.

Cassianella sexradiata (Branson). Ciriacks, 1963, p. 45, pl. 5, figs. 5–7.

Aviculopecten sexcostatus (Stuckenberg). Muromtseva, 1984, p. 61, pl. 27, fig. 6; pl. 33, figs. 10–13.

Material.—Only one external mold of a left valve. Reg. no. HP 100093.

Description.—Shell small, 14 mm long and 14 mm high, strongly inflated; umbo narrow, orthogyrate, salient above the hinge margin and curving down over the hinge; anterior auricle rounded-trigonal, a little inflated and marked off from the disc by a deep and wide sulcus; posterior auricle imperfectly preserved, relatively small, obtuse-triangular, with its posterior margin weakly sinuated and set off from the disc by a strong, posterior, radial marginal rib; surface ornamented with nine slender but sharply raised radial ribs, projecting ventrally at ventral margin; interspaces between radials wide, slightly concave; distinct, regular concentric fila, closely spaced, curving dorsally in the interspaces, and with comarginal spinose projections on the radials; hinge margin straight, shorter than shell length; hinge not preserved.

Remarks.—The present specimen differs from the type in its more numerous radial ribs, but this is considered to be due to infraspecific variation. *Crassinoides sexcostatus* can be distinguished from *C. crassispinosus* (Chronic) by its weaker radial ribs and less spinose concentric sculpture, and from *C. rara* (Waterhouse) by the absence of secondary radial riblets.

Occurrence.—Black siliceous shale of the uppermost fossil horizon of the Hovtinden Member at Festningen (F11).

Superfamily Limacea Rafinesque, 1815

Family Limidae Rafinesque, 1815

Genus **Palaeolima** Hind, 1903

Palaeolima nakamurai sp. nov.

Figures 6–9, 10

Materials.—External casts and molds of a complete right valve and an incomplete left valve, and a nearly complete external cast of a right valve. Reg. nos. HP 100096 (holotype) and 100097. Holotype specimen occurs in shale of Unit 7 of the Hovtinden Member at Festningen.

Diagnosis.—Broadly rounded *Palaeolima* ornamented with wide, rounded, branching radial ribs intercalated with narrow furrows.

Etymology.—Dedicated to Dr. K. Nakamura, who surveyed West Spitsbergen several times as a leader of the Japanese Expedition.

Description.—Shell equivalve, inequilateral, a little inflated, broad and oblique-oval in shape, opisthocline, extended anteroventrally; umbo not prominent, a little salient above the hinge margin; apical angle about 110°; umbonal angle about 80°, no umbonal ridge; umbo situated near the middle of the straight hinge margin; height slightly less than the length; both auricles obtuse-triangular, anterior one

Table 8. Measurements of *Palaeolima nakamurai* sp. nov. A: umbonal angle (angle between hinge line and longest axis of the shell)

| Reg. | no. | L | H | H/L | U | U/L | a | A | r | r ₁ | V | Hor. |
|------|--------|-----------------|------|------|------|------|----|-----|----|----------------|---|-------|
| HP | 100096 | 31.0 | 29.7 | 0.96 | 18.8 | 1.65 | 80 | 110 | 33 | 15 | R | F 7-1 |
| HP | 100097 | 24 ₊ | 24.5 | — | — | — | 80 | 110 | 30 | 16 | R | AP 6 |

depressed, obscurely defined from the main body; posterior one marked off anteriorly by a steep umbonal slope; surface ornamented with 15-16 broadly rounded, primary radial ribs wider than interstitials, increasing in number by bifurcation, reaching 30 or more in total; growth lines weak; anterior auricle nearly smooth; posterior one sculptured by weak radial costae; hinge not preserved.

Comparison.—The species is similar in ornament to *Palaeolima simplex* Hind (1903, p. 39, pl. 39, figs. 24-27) from the Carboniferous of England, *P. petaline* Zhang (1981, p. 213, pl. 11, figs. 17) and *P. fasciculicostata* Liu (1976, p. 236, pl. 17, figs. 22, 24, 25), both from the lower Upper Permian of South China. It is distinguished from them by its larger size and more circular outline. *Palaeolima krotowi* (Stuckenbergh, 1898, p. 336, pl. 1, fig. 29) from the Upper Carboniferous of Russia has radial ribs narrower than its interstitial furrows and is easily distinguished from the present species. Specimens referred to *P. krotowi* by Licharew (1927, p. 37, pl. 3, figs. 8-12, 14) and Muromtseva (1984, p. 79, pl. 33, fig. 11), from the Lower Permian of the Urals and Pechora, have broader radials than interstices, so the specific identification is doubtful. These shells are more similar to the present new species than to *P. krotowi*, but they differ from it being more anteroventrally extended and more oblique in shape.

Occurrence.—Rare in black shale of the lower part of the Hovtinden Member at Festningen (F 7-1) and at Ahlstrandodden (AP 6).

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An early Late Cretaceous mammal from Japan, with reconsideration of the evolution of tribosphenic molars

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Abstract. The morphology of a mandibular fragment with a left lower molar discovered in the “Upper Formation” (upper Cenomanian lower Turonian) of the Mifune Group in central Kyushu, southwestern Japan, suggests that this fossil should be assigned to a new species of Late Cretaceous mammal, *Sorlestes mifunensis* sp. nov. (Infraclass Eutheria ; Order Proteutheria ; Family Zhelestidae). *S. mifunensis* is the oldest zhelestid yet recorded. Some workers suggest that the Zhelestidae have a close affinity with ungulates. A detailed comparison between the lower molar of the new species and those of ungulates supports this suggestion. The comparison also suggests that the Zhelestidae have a closer affinity with ungulates than the Zalambdalestidae and other contemporary mammals, and that *S. mifunensis* has a relatively primitive character within the Zhelestidae. This comparison leads us to revise the diagnoses of the family Zhelestidae and of the genus *Sorlestes*. The unique character of the entoconid-hypoconulid twinning seen in the Zhelestidae was probably caused by the movement of the hypoconid (the presumed first single talonid cusp seen in the first therian *Kuehneotherium*) to the buccal side, far away from the other talonid cusps. This twinning pattern is distinct from the twinning pattern seen in marsupials.

Key words : Japan, Late Cretaceous, Mesozoic mammal, Mifune Group, *Sorlestes*, tribosphenic molar

Introduction

It is generally believed that tribosphenic mammals first appeared around the Jurassic–Cretaceous boundary (Bown and Kraus, 1979 ; Kielan-Jaworowska *et al.*, 1979b ; Sigogneau-Russell, 1991). They are ancestors of the eutherian and metatherian mammals which probably differentiated during the Neocomian (Early Cretaceous) (Kielan-Jaworowska *et al.*, 1979a ; Cifelli, 1993 ; Eaton, 1993 ; Wang *et al.*, 1995). The eutherian orders radiated widely at the beginning of the Tertiary. However, recent fossil finds suggest that the eutherian orders may have originated and differentiated in the Late Cretaceous (Fox and Youzwysyn, 1994 ; Archibald, 1996 ; Gheerbrant *et al.*, 1996).

Until 20 years ago there were only very few reports of tribosphenic mammals from the early Late Cretaceous (Cenomanian–Santonian). This situation has, however,

changed and many such fossils are now known from this period (Cifelli and Eaton, 1987 ; Cifelli, 1993 ; Eaton, 1993 ; Nessov *et al.*, 1994 ; Nessov *et al.*, 1998). In particular, Nessov *et al.* (1994) report many early Late Cretaceous tribosphenic mammals from Middle Asia (Uzbekistan, Kazakhstan and Tajikistan).

In the present study, we document a mammal fossil specimen, which was first reported by Setoguchi (1992), from the “Upper Formation” (upper Cenomanian–lower Turonian ; lower Upper Cretaceous) of the Mifune Group in central Kyushu, southwestern Japan. The specimen is a small mandibular fragment with a tribosphenic lower molar. The new find is significant because it is the only known example of a mammal fossil from the Late Cretaceous eastern coastal lowlands of the Asian Continent. The other Asian Late Cretaceous mammal fossils, in contrast, come from either inland deposits or deposits along the Tethys sea and the

Turgai Strait of that time (Clemens *et al.*, 1979; Nesson *et al.*, 1994).

The tooth nomenclature used in this contribution is that of Bown and Kraus (1979) and Nesson *et al.* (1998).

Geological setting

The present fossil material was discovered in the "Upper Formation" of the Mifune Group, which is distributed in the Mifune Town area of Kumamoto Prefecture, central Kyushu, southwestern Japan (Figure 1). The Mifune Group unconformably overlies green schist associated with serpentinite in the northern area, and the Upper Permian Mizukoshi Formation in the southern area (Matsumoto, 1939). The Mifune Group is, in turn, unconformably overlain by the Upper Cretaceous Gankaizan Formation (Tamura and Tashiro, 1966). The Mifune Group is considered to be early Late Cretaceous in age (see below), and to have formed in a sedimentary basin situated on the east coastal margin of the Late Cretaceous Asian Continent.

The Mifune Group has a total thickness of about 1,500 m and consists of "Basal", "Lower" and "Upper" formations (Matsumoto, 1939). The lowermost or "Basal Formation" is

dominated by conglomerate and very coarse-grained sandstone (Matsumoto, 1939), yielding fresh-water bivalves, such as *Trigonioides*, (Tamura, 1979; Matsumoto *et al.*, 1982). The middle or "Lower Formation" is dominated by sandstone and sandy mudstone (Matsumoto, 1939), yielding brackish-water and shallow-marine molluscan fossils, such as *Inoceramus concentricus costatus* and *Eucalycoceras* sp. cf. *E. spathi* of middle Cenomanian age (Tamura and Matsumura, 1974; Tamura, 1979; Matsumoto *et al.*, 1982). The uppermost or "Upper Formation" is dominated by red mudstone (Matsumoto, 1939), yielding non-marine bivalves (Tamura, 1979) and several vertebrate fossils, such as dinosaurs, pterosaur, and the present specimen (Tamura *et al.*, 1991; Setoguchi, 1992; Okazaki and Kitamura, 1996).

The Gankaizan Formation, which unconformably overlies the Mifune Group, consists of conglomerate, coarse-grained sandstone and red mudstone (Tamura and Tashiro, 1966; Matsumoto *et al.*, 1982), yielding *Inoceramus* (*Platyceramus*) *amakusensis*, of lower Santonian age, in its upper part (Tamura and Tashiro, 1966; Matsumoto *et al.*, 1982).

The present fossil material comes from the upper part of the "Upper Formation" near the Amagimi Dam, Mifune Town (Figure 1). The stratum where the fossil was discovered

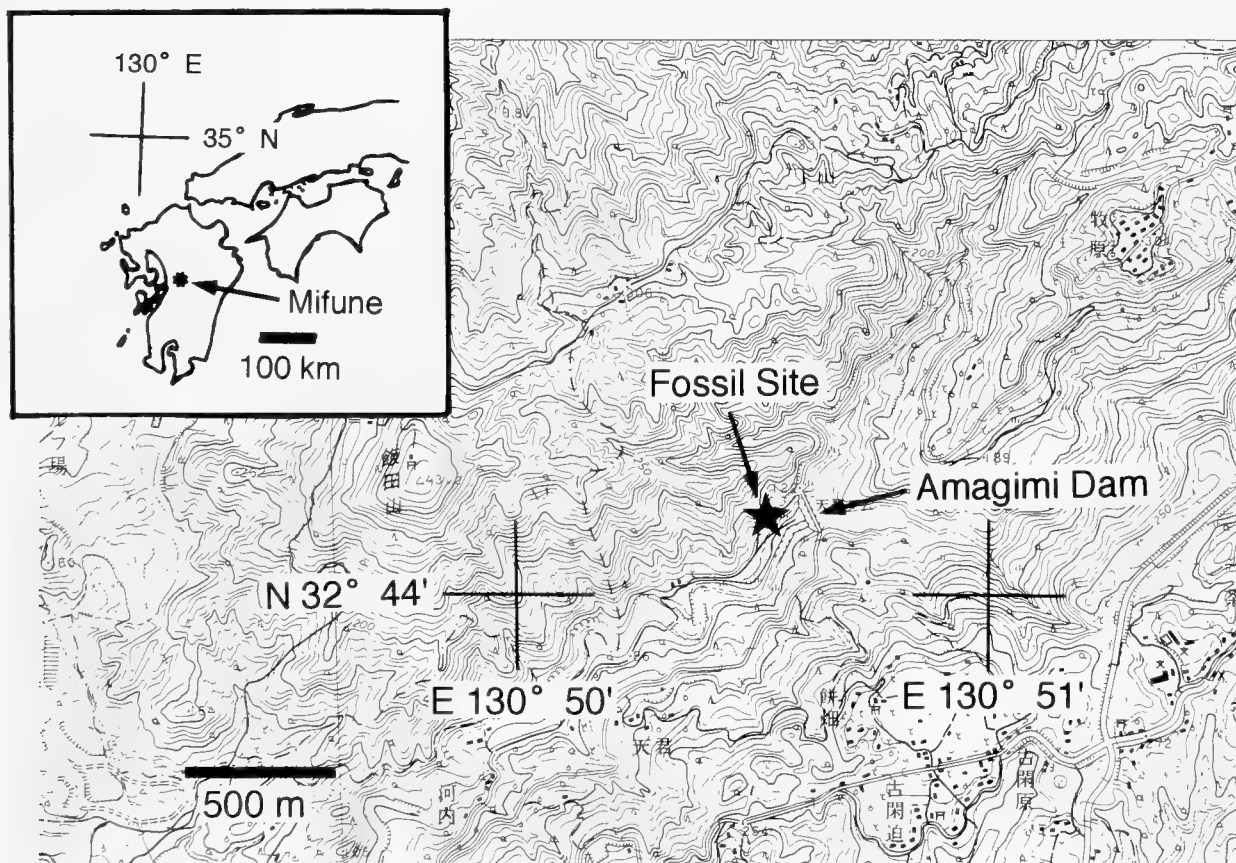


Figure 1. Topographic map showing the fossil locality, near the Amagimi Dam, Mifune Town, Kumamoto Prefecture, Kyushu, southwestern Japan (a part of topographic map "Mifune", 1 : 25,000 scale, Geographical Survey Institute of Japan).

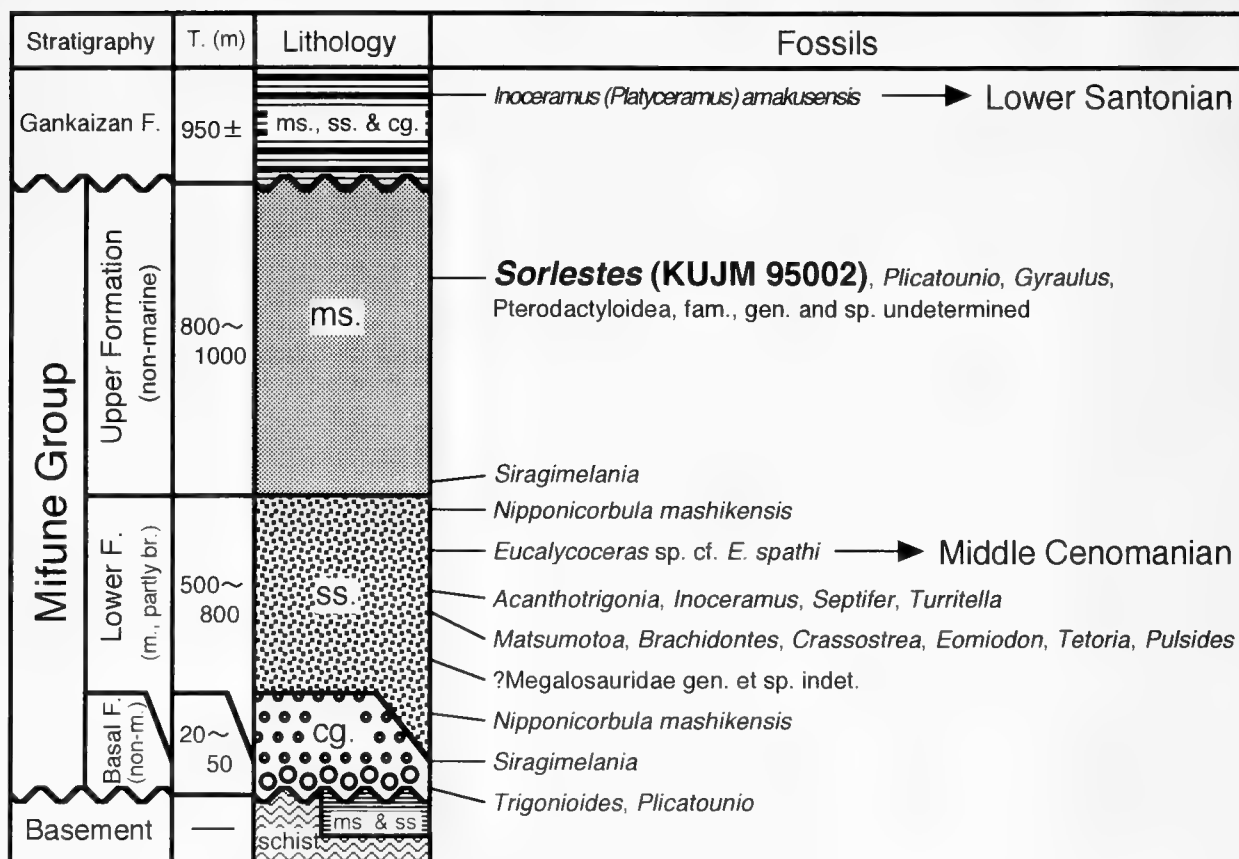


Figure 2. Stratigraphy of the Cretaceous deposits in the south of Kumamoto City, Kyushu, Japan (modified from Matsumoto, 1939; Tamura and Tashiro, 1966; Matsumoto *et al.*, 1982; Tamura *et al.*, 1991; Hasegawa *et al.*, 1992; Okazaki and Kitamura, 1996). Abbreviations: m., marine; br., brackish; T., thickness; ms., mudstone; ss., sandstone; cg., conglomerate.

consists of coarse grained sandstone. The age of the "Upper Formation" is considered to be late Cenomanian to early Turonian on the basis of the ages of the Lower Formation and the Gankaizan Formation. A synthetic scheme of the stratigraphy of the Mifune Group is shown in Figure 2.

Systematic paleontology

Class Mammalia Linnaeus, 1758
Infraclass Eutheria Gill, 1872
Order Proteutheria (Romer, 1966) Butler, 1972
Family Zhelestidae (Nessov, 1985) Nessov, 1990

Revised diagnosis.—The upper and lower molars are typical tribosphenic types. The protocone is large and mesiodistally expanded. The styler shelf is relatively narrow, but the parastylar region is wide and expanded mesially bearing two cusps. A small paraconid is displaced relatively lingually and relatively close to the metaconid. Compared with other proteutherians, the trigonid height is lower relative to talonid height. The talonid is about as wide as the trigonid and mesiodistally longer and lower than the trigonid.

The talonid basin is deep and open lingually, so that the deepest part of the talonid basin is situated at its lingual margin. The entoconid and hypoconulid are markedly close to one another, and are quite clearly separated from the hypoconid.

The upper and lower last premolars are premolariform (*sensu* Krishtalka, 1976), but the upper one has a incipient metacone. In occlusal view, the upper one is somewhat mesiodistally constricted between the paracone and the protocone.

Genus ***Sorlestes*** Nessov, 1985

Type species.—*Sorlestes budan* Nessov, 1985.

Included species.—*S. budan* Nessov, 1985; *S. kara* Nessov, 1993; *S. mifunensis* sp. nov.

Revised diagnosis.—The paraconid is not strongly appressed to the metaconid. The protoconid is larger than in *Aspanlestes* (Zhelestidae). The entoconid is very markedly close to the hypoconulid (entoconid-hypoconulid twinning), and both are located at the distolingual corner of the talonid, opposite the hypoconid which is located at the distobuccal corner. The cristid obliqua extends just below the notch of

the protocristid between the protoconid and the metaconid.

***Sorlestes mifunensis* sp. nov.**

Figure 3

Holotype.—KUJM 95002, a left mandibular fragment with a molar. (KUJM means Kyoto University, Japan, Mesozoic)

Hypodigm.—The type specimen only.

Etymology.—Named after Mifune Town, where the type specimen was discovered.

Repository.—Department of Geology and Mineralogy, Division of Earth and Planetary Sciences, Graduate School of

Science, Kyoto University, Japan.

Locality.—Lat. 32°44'09" N; Long. 130°50'32" E: Loc. 1 of Tamura *et al.* (1991, fig. 1; Figure 1), near the Amagimi Dam, Mifune Town, Kumamoto Prefecture, Kyushu, southwestern Japan.

Horizon.—Upper part of the "Upper Formation", Mifune Group (Figure 2).

Age.—Late Cenomanian to early Turonian; Late Cretaceous.

Diagnosis.—The lower molar of *S. mifunensis* is almost as large as *S. budan*, and larger than *S. kara*. Compared to *S. budan*, the paraconid is less appressed to the metaconid, and the entoconid and hypoconulid are closer together.

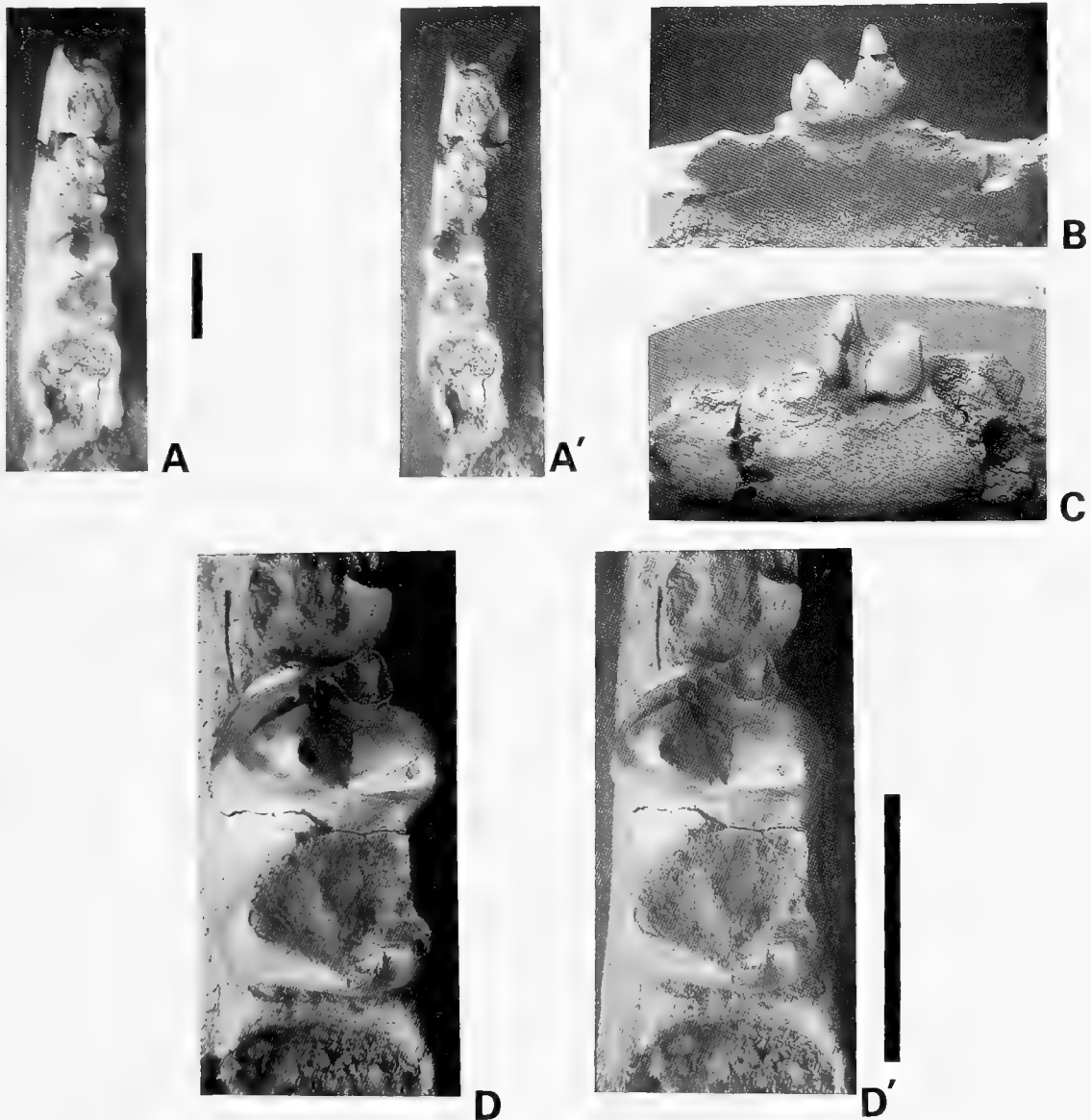


Figure 3. *Sorlestes mifunensis* sp. nov., KUJM 95002, holotype. **A, A'**, occlusal view (stereophotographic pair). **B**, lingual view. **C**, buccal view. **D, D'**, occlusal view of the preserved molar (stereophotographic pair). Scale bars=2 mm (left scale corresponds to A, A', B, C, right scale corresponds to D, D').

Description.—The type specimen (KUJM 95002) is a fragmentary left mandible with a molar. The preserved part of the mandibular ramus is about 8 mm in length, and about 4 mm in height and about 2 mm in width below the preserved molar. Immediately mesial to the molar, there is a broken root, which is circular and not compressed anteroposteriorly in occlusal view (Figures 3–A, A'). Immediately distal to the molar, there is a broken alveolus. Mental foramen could not be identified in KUJM 95002.

The protoconid of the preserved molar is much larger and higher than the metaconid, and leans somewhat lingually. The metaconid is situated just lingual to the protoconid. Although badly broken at the base, it is clear that the paraconid is near the anteroposterior midline, and less anteriorly appressed than in *S. budan*. There is no crest joining the paraconid with the metaconid. A distinct precingulid runs downward from the mesiobuccal base of the paracristid notch, disappearing at the buccal base of the protoconid. The posterior trigonid wall is almost vertical, and nearly perpendicular to the mandibular extension.

The talonid is longer than wide. It is longer than, as wide as, and roughly half as tall as the trigonid. The hypoconid and entoconid are almost the same height, and somewhat higher than the hypoconulid. The hypoconulid is only very slightly projected posteriorly. The entoconid and hypoconulid are closer together than in *S. budan*, and are located at the distolingual corner of the talonid. A very weak postcingulid runs down buccally from the hypoconulid, disappearing at the buccal base of the hypoconid. The deepest part of the

talonid basin is situated at its lingual margin, so that the deep talonid basin is open lingually, and inclined lingually as a whole. The cristid obliqua originates directly below the notch between the protoconid and the metaconid, and is much higher than the entocristid. The hypoflexid is well-formed and deep.

Wear facets can be observed from the tip of the protoconid to the tip of the metaconid through the protoconid. The tips of the hypoconid, hypoconulid and entoconid are slightly worn. The talonid basin is also worn (although the effects of secondary erosion are difficult to assess), which forms a U-shaped “wear facet”.

Dental measurements are given in Table 1 and Figure 4.

Discussion

Identification of the present lower molar

The tooth class of the molar preserved in KUJM 95002 can be identified as M_2 , because the trigonid is as wide as the talonid which is the same as on M_2 of *S. budan*. The possibility that it should be identified as M_1 cannot, however, be immediately excluded. As Lillegraven (1976) pointed out, it is a usual therian condition that the paraconid is most buccally set on M_1 and becomes progressively more lingual on M_2 – M_3 . Furthermore, Cretaceous eutherians characteristically have a protoconid that leans somewhat more lingually on M_1 than that on M_2 , so the distance between the tip of the protoconid and that of the metaconid in occlusal view is shorter on M_1 than that on M_2 . These characters are also observed in the zhelestid *Aspanlestes* (Nessov *et al.*, 1994, pl. 4, fig. 1). KUJM 95002 shows a combination of these M_1 characters.

In either case, KUJM 95002 and *S. budan* clearly have distinct lower molar structures (see diagnosis of *S. mifunensis*). *S. kara*, another species of *Sorlestes*, has much smaller molar size than KUJM 95002. We, therefore, consider KUJM 95002 to be a new species of *Sorlestes*.

Phyletic position of *Sorlestes mifunensis*

Phylogenetic relationships of the Zhelestidae have been discussed by various workers (Figure 5). Lillegraven (1976) described *Gallolestes*, which was subsequently classified as belonging to the Zhelestidae by Nessov *et al.* (1994), based on the lower molar morphology. Lillegraven (1976) favors eutherian affinities for *Gallolestes*, and points out the similarities between *Gallolestes* and hyposodontid condylarths. Butler (1977), however, points out that *Gallolestes* shares some derived characters of the lower molars with *Zalambdalestes* (Proteutheria; Zalambdalestidae) and with *Purgatorius* (Primates), and he doesn't exclude the possi-

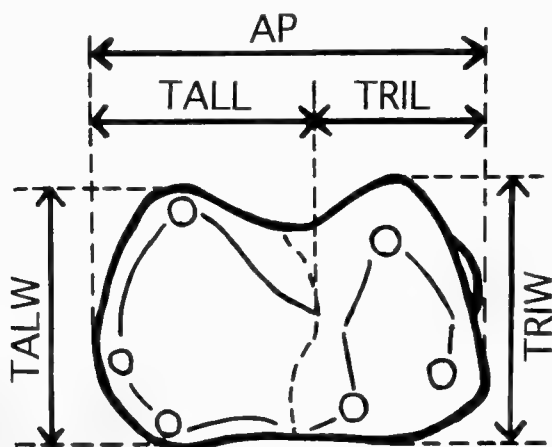


Figure 4. Orientations of the measurements of lower molars (modified from Nessov *et al.*, 1994). Buccal to top of page; anterior to right. Abbreviations are shown in Table 1.

Table 1. Measurements (in mm) of the preserved molars of the type specimens of *Sorlestes mifunensis* sp. nov. The measurements are oriented as shown in Nessov *et al.* (1994, fig. 1; see Figure 4). Abbreviations: AP, anteroposterior length; TRIL, trigonid length; TALL, talonid length; TRIW, trigonid width; TALW, talonid width.

| | [mm] | AP | TRIL | TALL | TRIW | TALW |
|--|------|------|------|------|------|------|
| KUJM 95002 (<i>S. mifunensis</i>) left lower molar (M_1 or M_2) | | 2.60 | 1.15 | 1.45 | 1.75 | 1.70 |

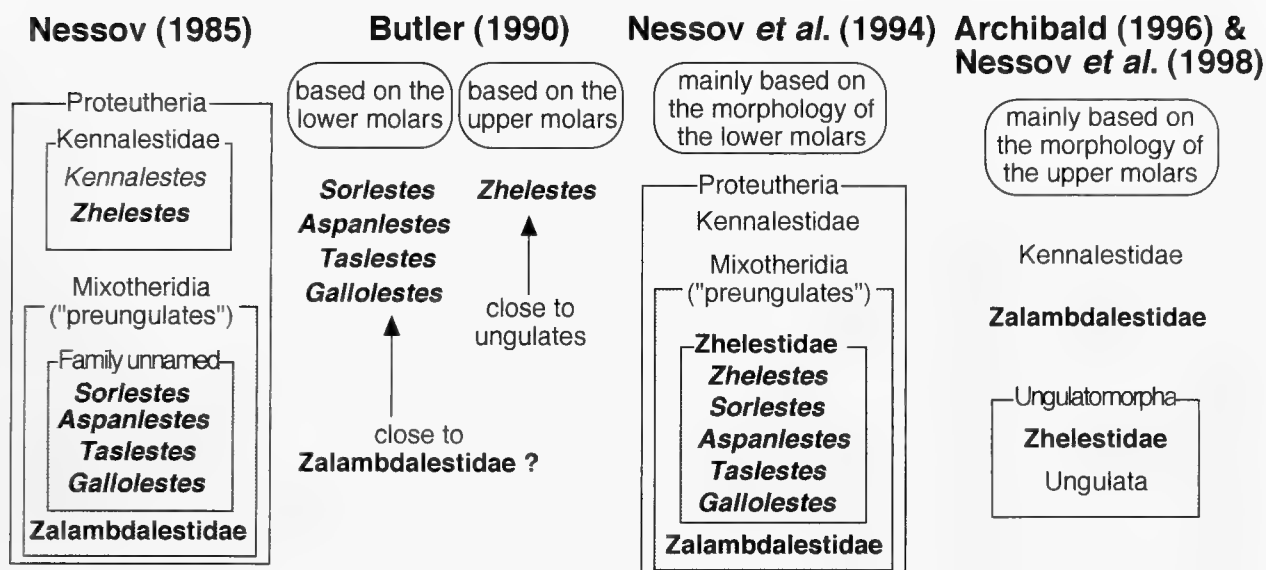


Figure 5. The classifications and phylogenetic relationships used in recent studies for the Zhelestidae.

bility of a relationship between *Gallolestes* and *Protungulatum* (Condylarthra). Clemens (1980) concludes that *Gallolestes* is possibly a representative of another lineage of metatherian-eutherian grade of dental evolution that cannot be assigned to either the Eutheria and Metatheria.

Based on the lower molar morphology, Nesson (1985) suggests that *Taslestes*, *Aspanlestes*, *Sorlestes* and *Gallolestes* should be combined in the same taxonomic group, a group which was subsequently classified as belonging to the Zhelestidae in Nesson et al. (1994). Nesson (1985) proposed a new suborder Mixotheridia (Proteutheria) including both the above genera and the Zalambdalestidae, and suggested that this suborder was related to condylarths. In the same paper, he described a new genus *Zhelestes*, based on the upper dentition. He classified it into the new subfamily Zhelestinae (Proteutheria; Kennalestidae), and at this time didn't include it in the Mixotheridia. Later, he raised this subfamily to the family level (Nesson, 1990). Butler (1990) points out that the zalambdalestids differ from *Aspanlestes*, *Sorlestes* and *Gallolestes* in some molar features, suggesting that relationships of these genera to zalambdalestids is not impossible, but it needs to be substantiated. He also considers that *Zhelestes* might be an earlier representative of condylarths. According to Nesson et al. (1994), the Zhelestidae include *Gallolestes*, *Taslestes*, *Aspanlestes* and *Sorlestes*, and these are all included in the suborder Mixotheridia along with the Zalambdalestidae. They consider the Mixotheridia (both the Zhelestidae and the Zalambdalestidae) to be "preungulates". In contrast, based mainly on the upper molar's morphology, Archibald (1996) and Nesson et al. (1998) consider that the Zhelestidae are sister groups of ungulates, and the Zalambdalestidae are only distantly related to them.

In this paper, we follow the suggestions of Archibald (1996) and Nesson et al. (1998). The reasons for our preference are briefly summarized below.

On the basis of the lower molar structure, Nesson et al. (1994) claimed that both the Zhelestidae and the Zalambdalestidae are closely related to ungulates. However, the two families show the following differences: (1) The Zhelestidae have more low-crowned lower molars with a trigonid that is less elevated to the talonid (Butler, 1990). (2) The paraconid and metaconid in the Zhelestidae are less closely appressed than in the Zalambdalestidae. (3) The Zhelestidae have a lingually open talonid, whereas the talonid is lingually closed in the Zalambdalestidae (see Kielan-Jaworowska, 1984, pl.14,15). In these features, the Zhelestidae are morphologically more similar to early ungulates than to the Zalambdalestidae. Most early ungulates (for instance, *Protungulatum*, *Diacodexis*, and so on) share the diagnostic characteristics of zhelestids, that is, the high, large, wide and lingually open talonid with the hypoconulid situated markedly close to the entoconid, and the rather lingually displaced paraconid with some appression to the metaconid (see McKenna, 1960, figs. 52, 53, 56, 57; Archibald, 1982, figs. 56, 60; Estravis and Russell, 1989, pl.1; Rose, 1996, fig.1). This combination of characteristics is not seen in any other contemporary mammal. For example, in *Purgatorius*, an early primatomorphan, the talonid is large, wide and high, but is closed lingually with the hypoconulid situated centrally (see Clemens, 1974, fig.2; Buckley, 1997, fig.1). In *Gypsonictops*, a Late Cretaceous insectivore, the talonid is large, wide and somewhat lingually open. However, the hypoconulid is centrally situated, and the paraconid is situated rather centrally than lingually (see Clemens, 1973, figs. 1, 4; Cifelli, 1990, fig. 2).

Based mainly on an analysis of upper molar morphology, Archibald (1996) and Nesson et al. (1998) suggest that the Zalambdalestidae does not have a close affinity with ungulates. Similarly, a study of lower molar morphology indicates that the Zhelestidae most closely resemble early ungulates. The lingually closed talonid in the Zalambda-

lestidae, which is shared by many other eutherians, may be an apomorphic character which zhelestids and early ungulates do not possess (see below). This would imply that the Zalmalestidae should be excluded from a very close relationship with ungulates. In support of this idea, some workers (Van Valen, 1964; McKenna, 1975; Stucky and McKenna, 1993; Archibald, 1996) consider the Zalmalestidae to be more closely related to *Anagale* and rabbits.

Compared with the Zhelestidae, early ungulates have a relatively high talonid with robust cusps on the lower molars. Compared to the other representatives of the Zhelestidae, *Sorlestes mifunensis* shows a primitive characteristic in that the paraconid is less appressed to the metaconid.

Nessov (1993) created a new family Kulbeckiidae (consisting of a single new genus *Kulbeckia*) within the Mixotheriidae. In the Kulbeckiidae, the hypoconulid is markedly close to the entoconid, and the paraconid is lingually situated with appression to the metaconid, similar to the Zhelestidae. Unfortunately, it is not clear whether the talonid is open or not in the Kulbeckiidae, so it is difficult to discuss any possible relationship between the Zhelestidae, Kulbeckiidae and other mammals.

Evolution of tribosphenic molars

The most characteristic feature of *Sorlestes mifunensis* is the lower molar with the hypoconulid situated markedly close to the entoconid, quite clearly opposed to the hypoconid. This twinning pattern is rarely seen in other Cretaceous eutherians, in which the hypoconulid is centrally-located between the hypoconid and the entoconid. The recognition of this character prompted us to reconsider the evolution of the talonid cusps. It seems that the talonid cusps developed along with the occluding upper tooth and the adjacent lower tooth.

1. First cusp formed in the talonid of *Kuehneotherium*, the first therian mammal: The earliest therian mammal, *Kuehneotherium*, had already appeared by the Norian (Late Triassic) (Fraser *et al.*, 1985). In the lower molars of *Kuehneotherium*, the tallest and largest cusp can be recognized as homologous with the protoconid of the later tribosphenic molars. The other two cusps, which are situated mesiolingually and distolingually from the protoconid, can likewise be identified as equivalents of the paraconid and metaconid, respectively (Kermack *et al.*, 1968). These homologies of the trigonid cusps are now not really in debate (Slaughter, 1971).

In the lower molars of *Kuehneotherium*, there is, however, a unicuspid distal heel or talonid, posterior to the trigonid (Kermack *et al.*, 1968, fig. 3). The homology of this cusp has been discussed by several workers (Slaughter, 1971; Clemens and Lillegraven, 1986), and the two main opinions are that it corresponds to either the hypoconid or hypoconulid.

Mills (1967) used the occlusal relationship between the upper and lower molars to propose that the single talonid cusp of Jurassic pantotheres corresponds to the hypoconid on the basis of the occlusal relationship between the upper and lower molars. The same conclusion was also reached by Freeman (1979) and Prothero (1981). In contrast, Kermack

(1967) interpreted the single talonid cusp in Welsh pantotheres (*Kuehneotherium*) as the hypoconulid on the basis of the relationship between the talonid and its following tooth. Crompton (1971), Slaughter (1971) and Butler (1978) also correlated this cusp with the hypoconulid, although the latter didn't completely exclude the possibility that it could represent the hypoconid.

The next stage in evolution toward the tribosphenic molar is seen in *Amphitherium* or *Palaeoxonodon*, whose talonid extends distobuccally from the base of the metaconid and bears a large single cusp at its distobuccal margin (Simpson, 1928, fig. 38; Freeman, 1979, pls. 16, 17). In *Palaeoxonodon*, there is a small cuspule at the approximate median point of the oblique crest which links the metaconid and a large single talonid cusp (Freeman, 1979). Further development is seen in *Peramus*. In this genus the talonid bears two or three cusps, identified as the hypoconid, hypoconulid and entoconid of the tribosphenic molar (Clemens and Mills, 1971; Clemens and Lillegraven, 1986). The talonid basin is not fully basined and is open lingually (Clemens and Mills, 1971, pl. 3).

By comparing the molar morphology of the animal mentioned above with later tribosphenic mammals, we consider that the single talonid cusp seen in *Kuehneotherium* corresponds to the hypoconid, as proposed by Mills (1967). This suggestion is also supported by the following arguments. (1) We would like to stress the occlusal relationship between the upper main cusp (paracone) and the first talonid cusp. The paracone is the largest cusp in the upper molar and is functionally very important for masticating foods. We, therefore, propose that the occlusal relationship between the paracone and the single talonid cusp, as well as between the paracone and the protoconid, is likely to be maintained in the therians. (2) In *Amphitherium* or *Palaeoxonodon*, the talonid extends distobuccally from the base of the metaconid and bears a large single cusp at its distobuccal margin, where the hypoconid of the tribosphenic molar is situated. (3) We propose, furthermore, that the groove separating the hypoconid and the hypoconulid in tribosphenic molars is also significant. This groove is deeper and stronger than the groove separating the hypoconulid and the entoconid, so the hypoconulid and entoconid are likely to be related more closely to each other than to the hypoconid. (4) Freeman (1979) stated that in certain specimens of *Palaeoxonodon* there is an incipient development of the entoconid and hypoconulid in addition to the large talonid cusp situated distobuccally.

We, therefore, propose the following sequential development. The first talonid cusp seen in *Kuehneotherium* corresponds to the hypoconid, and the entoconid and hypoconulid appeared at some later stage, being more closely related to each other than to the hypoconid.

2. Entoconid hypoconulid twinning: The primitive talonid for a tribosphenic molar envisaged by most workers is basined and lingually opened with a relatively large hypoconid, smaller hypoconulid and in some cases also an entoconid (Clemens and Lillegraven, 1986; Szalay, 1994). Examination of Early Cretaceous tribosphenic mammals suggests that the roughly centrally-placed hypoconulid

between the hypoconid and the entoconid may also be a primitive characteristic.

In Late Cretaceous mammals, the lower molars of many eutherians have a centrally-placed hypoconulid. In contrast, the molars of contemporary marsupials have a hypoconulid twinned with an entoconid. In this respect the molars of the eutherian Zhelestidae resemble those of marsupials. However, the twinning in the Zhelestidae is clearly distinct from that in marsupials (Figure 6).

In marsupials, the hypoconulid is distolingually displaced compared to the Zhelestidae. The twinning pattern seen in the Zhelestidae is associated with a primitive-type talonid as seen in the tribosphenic pattern. This association suggests that the twinning seen in the Zhelestidae is more primitive than in marsupials. The twinning pattern seen in the Zhelestidae is likely to have been caused by the movement of the hypoconid to the buccal side far away from the other talonid cusps, corresponding to the expansion of the protocone of the upper molars (Archibald, 1996; Nessov *et al.*, 1998). The twinning pattern seen in marsupials is more likely to be a secondary feature (Cifelli, 1993), and could be functionally related to the early trend of the enlargement of the metacone and reduction of the paracone in this group (Clemens and Lillegraven, 1986).

The entoconid-hypoconulid twinning is also related to the position of the paraconid of the posterior molar. This is because the paraconid fits into the groove between the hypoconulid and the entoconid of the anterior tooth. In many eutherians, the paraconid is situated centrally,

because the hypoconulid of the anterior tooth is centrally-placed between the hypoconid and the entoconid, and the groove between the hypoconulid and the entoconid is situated more buccally. In the Zhelestidae, the paraconid is situated more lingually than centrally, because the hypoconulid is situated lingually and twinned with the entoconid, and the groove between the two cusps is situated more lingually than centrally. In marsupials, the paraconid is situated more mesiolingually than in eutherians (include the Zhelestidae), because the hypoconulid of the anterior tooth is situated more distolingually and twinned with the entoconid, and the groove between the two cusps is situated far more distolingually.

As mentioned above, the lingually open talonid with a hypoconulid markedly close to the entoconid as seen in the Zhelestidae is probably a reflection of the primitive state. This condition is also seen in early eutherian like *Prokennalestes* (Kielan-Jaworowska and Dashzeveg, 1989, figs. 26, 27), but not seen in early metatherian, *Kokopellia* (Cifelli, 1993, fig. 1).

Co-evolution of mammals and plants

The age from the Albian to the Cenomanian was a very important period for the mammalian evolution. At this time the flora underwent a change from one dominated by ferns and gymnosperms to one with abundant angiosperms. Flowering angiosperms appeared at the beginning of the Cretaceous, and very rapidly became a major plant group (Crane, 1987; Collinson, 1990). Angiosperms have leaves,

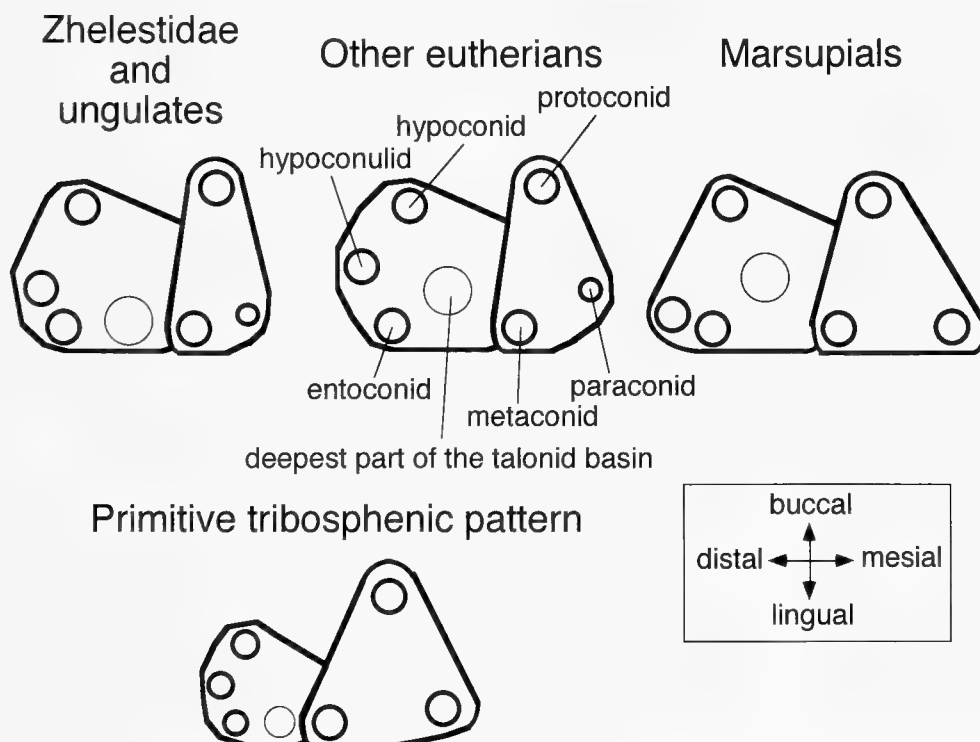


Figure 6. Comparisons of the lower molar patterns of tribosphenic mammals (occlusal view of the left lower molars).

flowers, fruit, pollen and honey. In other words, these plants have foods with high nutritive value. It was for this reason that insects began to evolve explosively at this time. It follows, therefore, that insectivorous mammals, whose staple foods were insects and/or larvae of insects, also began to increase in numbers and diversity. The mammals who began to diversify and radiate in this way are the Cretaceous tribosphenic mammals. The period when the Mifune Group was deposited is the very period when angiosperms had become a major plant group, and when insectivorous mammals like *Sorlestes* evolved rapidly.

Conclusions

Morphological studies of the mammalian remain discovered from the lower Upper Cretaceous Mifune Group in central Kyushu, southwestern Japan suggest that it should be assigned to a new species of the genus *Sorlestes* (Order Proteutheria; Family Zhelestidae), and is here named *S. mifunensis*.

The lower molars of the Zhelestidae exhibit a series of ungulate-like characteristics. It suggests that the Zhelestidae and early ungulates are far more closely related to each other than to the Zalambdalestidae and other mammals. The twinning pattern of the hypoconulid and entoconid in the Zhelestidae, including *Sorlestes mifunensis*, shows a more primitive state than that of metatherians and most of the other eutherians.

Sorlestes mifunensis is the oldest known zhelestid yet recorded, and suggests that the origin of ungulates perhaps goes back even further to the early Late Cretaceous, or at least, that mammals having ungulate-like characters had already been differentiated by the late Cenomanian to early Turonian. The find of *Sorlestes mifunensis* also indicates that zhelestid existed not only in western Asia but also on the coastal plain of eastern Asia.

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A new cheirolepidiacean conifer from the Lower Cretaceous (Albian) of Hokkaido, Japan

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Abstract. A new fossil conifer, *Pseudofrenelopsis glabra* sp. nov., (Cheirolepidiaceae) is described based on a single specimen obtained from the Lower Cretaceous Yezo Group (Albian) of Hokkaido, Japan. The new species is characterized by cuticle possessing thin periclinal walls, a well-developed hypodermis, and absence of trichomes on internode and outer leaf surface. Recently, the author described *Frenelopsis pombetsuensis* from the Lower Cretaceous Yezo Group (Albian) of Hokkaido. The family Cheirolepidiaceae is a diagnostic taxon of the Ryoseki type element that is reported only from the Ryoseki- and the Mixed-type floras. Thus *Pseudofrenelopsis glabra* is the second evidence of the Ryoseki-type element from Hokkaido.

Key words : Albian, conifer, Hokkaido, Middle Yezo Group, *Pseudofrenelopsis glabra*, Ryoseki-type floras.

Introduction

Jurassic and Early Cretaceous floras in eastern Eurasia have been classified by Kimura (1980, 1987) and Ohana and Kimura (1995) into three characteristic floras, the Ryoseki- and the Tetori-type floras, and the Mixed-type floras comprising elements of both the Ryoseki- and the Tetori-type floras. According to these authors, the Ryoseki-type floras grew under tropical to subtropical conditions with an annual long arid season, while the Tetori-type floras grew under temperate and moderately humid conditions.

The genus *Pseudofrenelopsis* belongs to the extinct conifer family Cheirolepidiaceae. Although this family is a dominant group of Mesozoic conifers, its closer affinity remains equivocal. The members of the family have various kinds of shoot morphology ranging from *Brachyphyllum-Pagiophyllum*-type shoots bearing scale leaves to *Frenelopsis-Pseudofrenelopsis*-type cylindrical segmented shoots bearing minute leaves. The single most reliable character of this family is possession of the pollen of the genus *Classopollis* Pflug (Watson, 1988). Although the plants yielding fossil remains attributed to the genus *Pseudofrenelopsis* were widely distributed during the Early Cretaceous (Berriasian-Albian) of North America, Europe, North Africa and Asia, they were apparently restricted to the Cretaceous (Table 1).

The frenelopsids, which include the genus *Pseudofrenelopsis* and the closely related genus *Frenelopsis*, have been used as indicator taxa of tropical to subtropical arid climate (Alvin, 1982). In east Asia the occurrence of the frenelopsids in fossil floras is restricted to the Ryoseki- and the Mixed-type floras. Although *Frenelopsis* is known from

the Ryoseki-type floras of the Upper Jurassic to Lower Cretaceous in Japan, fossil remains assigned to *Pseudofrenelopsis* have not been reported yet. In the present paper, the remains of shoot and associated cuticular features of *Pseudofrenelopsis* from Japan are described.

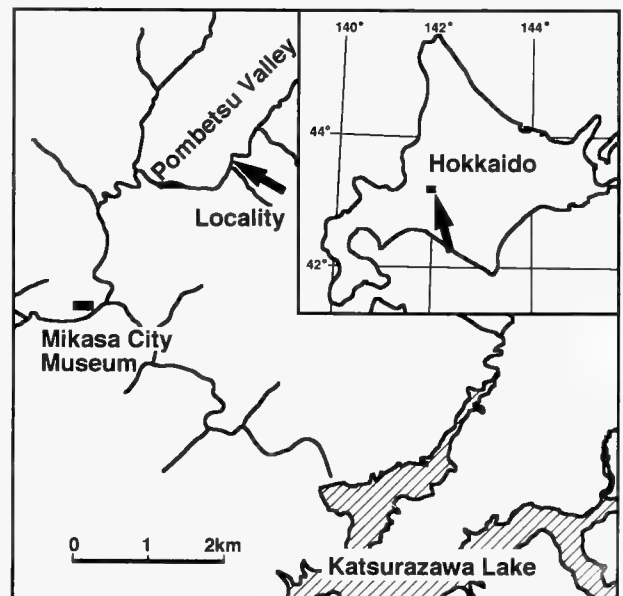
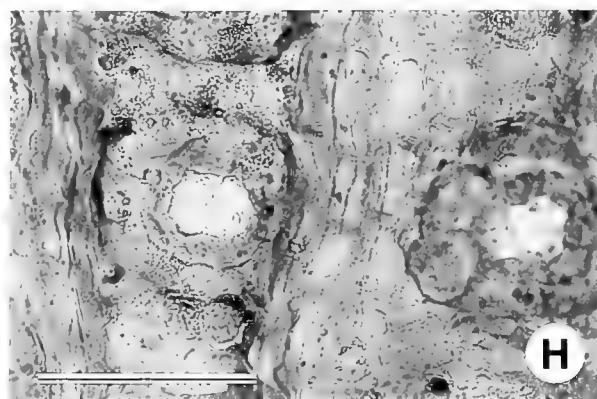
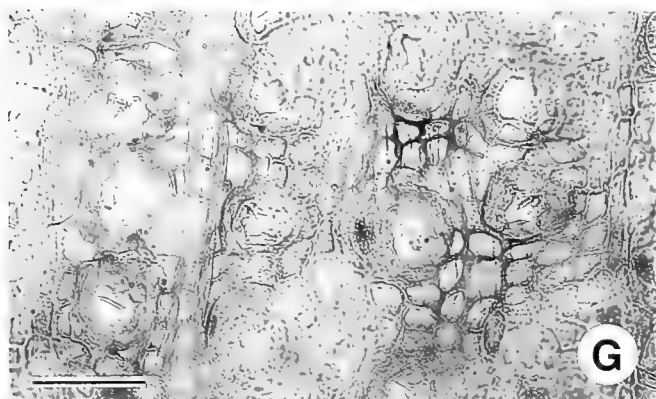
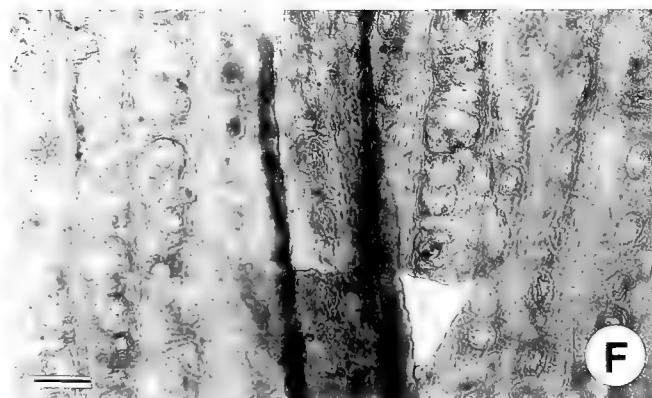
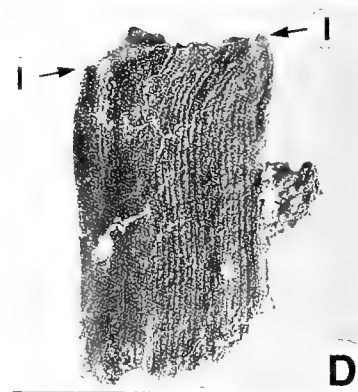
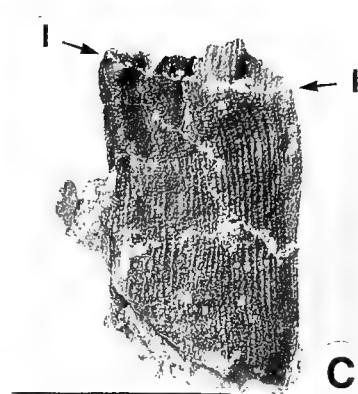


Figure 1. Map of Hokkaido, Japan showing the location of the Pombetsu Valley.



Material and Methods

Material.—A compressed conifer shoot was found in the Pombetsu Valley about 60 km northeast of Sapporo (Figure 1). The specimen was obtained from the mudstone bed of the so-called "Main part of Middle Yezo Group". The locality is situated between Matsumoto's outcrops Ik 2025 and 2031, from where the Albian ammonite *Ammonoceratites yezoensis* Yabe has been reported (Matsumoto, 1965, fig. 3).

Methods.—Fossil remains were immersed in Schulze's solution followed by diluted NaOH. The cuticle was mounted in Eukitt for light microscopy. For SEM observation, cuticles were coated with Pt-Pd in a Hitachi E-1030 ion sputter and photographed with Hitachi S-800.

All specimens used in this study are deposited in the Mikasa City Museum (MCM), Ikushumbetsu-nishikicho, Mikasa, Hokkaido.

Systematic description

Order Coniferales

Family Cheirolepidiaceae Takhtajan, 1963

Genus *Pseudofrenelopsis* Nathorst, 1893

Remarks of the genus.—The diagnosis originally based only on the type species was emended by Watson (1977) after studying specimens of *Frenelopsis varians* Fontaine, which is now placed in this genus. Recently, Srinivasan (1995) emended the diagnosis of *Pseudofrenelopsis* based on new morphological characters of Puddledock material. Srinivasan's concept is followed here.

Pseudofrenelopsis glabra sp. nov.

Figures 2A–H, 3A–I

Material.—Holotype, MCM-P030

Horizon.—Main part of the Middle Yezo Group (Albian).

Type locality.—Pombetsu Valley, Mikasa, Hokkaido (Figure 1; ca. 43°16'31"N, 141°59'20"E). The locality is about 80 m south of Matsumoto's (1965) outcrop Ik 2031.

Diagnosis.—Segmented shoot bears a simple spiral of leaves, each leaf encircling the stem. Leaf margin having hairs; outer surface of both abaxial and adaxial leaf cuticle smooth, without trichomes. Internode cuticle well developed. Outer surface of cuticle smooth, nonpapillate. Stomata arranged in longitudinal rows. Stomatal complex consisting of a pair of guard cells and 7–9 subsidiary cells. Guard cells sunken below a ring of subsidiary cells with irregularly oriented apertures. Stomatal pit rounded in surface view. Outer surface of subsidiary cells forming a raised

rim bounded by a deep groove around stomatal pit. A well developed cutinized hypodermis of thin-walled cells covering most of the internal surface of the cuticle.

Description.—A single compressed shoot was obtained (Figures 2A, B). The shoot is segmented, bearing a simple spiral of leaves. Each of the leaves encircles the stem. The internode is 6–9 mm long and 4 mm wide (Figures 2A, B). Triangular part of the leaf is up to 1.5 mm high at a node (Figures 2B, C; 3A). The leaf margin has hairs up to 40 μ m long (Figures 2E; 3B, C). Outer surface of both abaxial and adaxial leaf cuticle is smooth, without trichomes (Figures 3B–D).

The internode cuticle is well developed, about 8 μ m in total thickness. The cuticle consists of outer periclinal epidermal wall about 3 μ m thick, anticlinal wall and thinly cutinized hypodermis (Figure 3E). No dorsiventrality is observed (Figure 2F). Stomata are about the same optical density as the rest of cuticle and are arranged in well marked longitudinal rows in 7–9 rows per mm. Each row of stomata is a single stoma wide. 70–100 per mm² in density. (Figures 2F, G; 3F, G). The bands of epidermal cells between the rows of stomata are 20–70 μ m (1–3 cells) wide, consist of longitudinally arranged epidermal cells. The epidermal cells are elongated rectangular to polygonal in shape, 25–50 μ m long and 10–25 μ m wide (Figures 2F, G; 3G). Outer surface of the cuticle is smooth, nonpapillate (Figure 3F).

The stomatal complex is 80–120 μ m in diameter, consists of a pair of guard cells and 7–9 subsidiary cells (Figure 3G). The guard cells are 40–70 μ m long and 10 μ m wide and are sunken below a ring of subsidiary cells. The aperture of the stoma is irregularly oriented (Figure 3G). The stomatal pit is about 30 μ m in diameter and is rounded in surface view (Figures 3F, H). Outer surface of the subsidiary cells forms a raised rim bounded by a deep groove around stomatal pit. Each of the subsidiary cells has a single papilla projecting into the stomatal pit (Figures 2H; 3F, H, I).

A well developed cutinized hypodermis of thin-walled cells cover most of the internal surface of the cuticle except for the region immediately beneath each stomatal apparatus. The hypodermal cells are rectangular or polygonal under the stomatal zone and are axially elongate rectangular under the nonstomatal zone (Figures 3E, G).

Discussion.—Due to the fragmentary nature of the fossil specimen the arrangement of the branch system of *Pseudofrenelopsis glabra* is uncertain. External and cuticular observations of the specimen clearly indicate the absence of a groove or suture separating the basal cushions, as seen in living species of the Cupressaceae.

Although the epidermal cells are clearly visible with light microscopy (Figure 2G), SEM microscopy of the inner surface of cuticle shows only hypodermis and stomatal complexes,

Figure 2. *Pseudofrenelopsis glabra* sp. nov. (MCM-P030). **A:** Holotype (MCM-P030). **B:** Middle region of the holotype showing leaf margins (I). **C, D:** Opposite sides of the same shoot fragment showing the margin of a single leaf (I). **E:** Light microscope image of the leaf margin showing short hairs. **F:** Light microscope image of cuticle from internodal region showing fold represented by central dark line, and cuticles of both sides of the compressed specimen. Arrangement of stomata and epidermal cells show no significant difference on both sides of the cuticles. **G:** Light microscope image of cuticle from the internodal region showing longitudinally arranged stomata, light microscope. **H:** Light microscope image of stomata, focused through the stomatal pit showing the papillae. Scale bars=5 mm in A–D; 100 μ m in E–H.

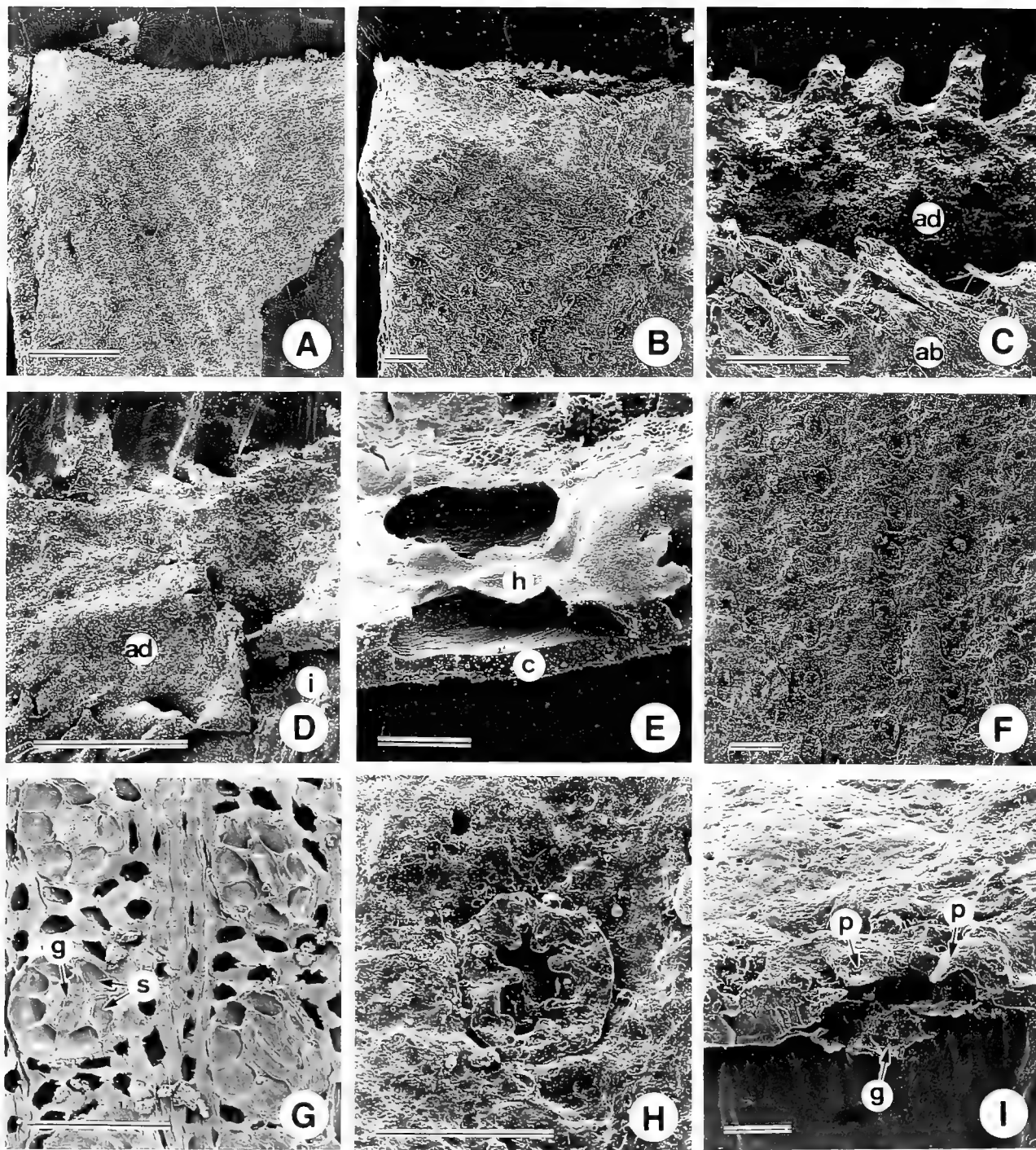


Figure 3. SEM micrographs of *Pseudofrenelopsis glabra* sp. nov. cuticle (MCM P030). **A**: Triangular free part of leaf. **B**: Edge of a leaf, showing marginal hairs and outer surface of abaxial leaf cuticle. **C**: Enlarged photo of 3B showing the short marginal hairs and smooth outer surface of the abaxial (ab) and adaxial (ad) leaf cuticle. **D**: Surface view of adaxial leaf cuticle (ad) and inner view of cuticle from the internodal region (i). **E**: Section of cuticle showing cutinized epidermis (c) and hypodermis (h). **F**: Outer view of cuticle from the internodal region showing mouth of stomatal pit. **G**: Cuticle from the internodal region showing longitudinally arranged stomatal complexes. Inner view of stomatal complexes showing the guard cells (g), and subsidiary cells (s). **H**: Outer view of a stoma showing the rounded mouth of the stomatal pit with papillae. **I**: Section of stoma showing guard cells (g), and papillae in throat of stoma (p). Scale bars = 500 μm in A, B; 50 μm in C, D, F-H; 10 μm in E, I.

Table 1 Comparative morphometrics of *Pseudofrenelopsis glabra* sp. nov. and related species.

| Characters/Species | <i>P. varians</i> | <i>P. parceramosa</i> | <i>P. papillosa</i> | <i>P. dalatzensis</i> | <i>P. heishanensis</i> | <i>P. nathorstiana</i> | <i>P. glabra</i> sp. nov. |
|---|---|--|---|-----------------------------------|------------------------|---|---------------------------|
| Internode length | 1.5–17 mm | 1–11 mm | 5–11 mm | 5.5–10 mm | 5–6 mm | 1.0–2.9 mm | 6–8 mm |
| Internode width | 3–7 mm | 1 mm < | 3–7.5 mm | 3–6.5 mm | 2.5–4 mm | 1.0–2.0 mm | 4 mm |
| Presence of suture or gap | none | in some 'open' form | none | none | none | yes | none |
| Maximum length of free leaf | 1.5 mm | 2 mm | 1.5 mm | 2 mm | 2 mm | 1.0 mm | 1.5 mm |
| Leaf margin | hairs up to 60 μ m | hairs up to 80 μ m | hairs up to 80 μ m | without hairs | without hairs | hairs up to 145.0 μ m | hairs up to 40 μ m |
| Trichomes or hairs on adaxial surface of leaf | hairs present | hairs present | hairs present | normally without hairs | without hairs | trichomes | without hairs |
| Internode cuticle thickness | 50–110 μ m | 30 μ m | 5–7.5 μ m | (5–)7.5–10(–25) μ m | 3–5 μ m | 10.0 μ m | 3 μ m |
| Trichomes or hairs on epidermal cells | up to 80 μ m | none to very long hairs | usually present | with large papillae | none | up to 200 μ m | none |
| Cutinized hypodermis | in "open" leaf-base cushions | well cutinized | none | none | none | none | well cutinized |
| Stomatal arrangement | scattered in "closed" form, rows in "open" form | well defined rows | longitudinal rows with scattered stomata | well defined rows | well defined rows | mostly ill defined rows | well defined rows |
| Density of stomatal rows | 8–10 per mm | 6–10 per mm | (4–)6–7(–9) per mm | (6–)7–8(–10) per mm | 8–9(–10) per mm | 11–12 per mm | 7–9 per mm |
| Diameter of stomatal apparatus | 70–100 μ m | 50–80 μ m | 40–92.5 μ m | 55–95 μ m | 62.5–100 μ m | 50–73 \times 54–62 μ m rarely 103.0 μ m | 80–120 μ m |
| Number of subsidiary cells | (4–)5–8(–9) | (4–)5–6(–7) | (4–)5–6(–8) | 5–6 | 5–6(–7) | (4–)5–6(–7) | 6–8 |
| Rim of stomatal pit | round: –with papillae | round: –with or without papillae | round: –with papillae | stellate | stellate | elliptical to round: –with papillae | round: –with papillae |
| Stratigraphic range | Albian | Berriasian–Albian | Lower Cretaceous | Lower Cretaceous | Albian | lower–mid–Albian | Albian |
| Distribution | North America | North America, Europe | China | China | China | China | Japan |
| References | Watson, 1977 | Alvin, 1977 Alvin et al. 1978 Watson, 1977 | Chow and Tsao, 1977 Zhou and Cao, 1979 Zhou, 1995 | Chow and Tsao, 1977 Zhou, 1995 | Zhou, 1995 | Srinivasan, 1995 | |

because the epidermal cells are covered by cutinized hypodermis (Figure 3G).

Comparison.—Although the present specimen is fragmentary, both external and cuticular features of the specimen correspond well with the diagnosis of *Pseudofrenelopsis* Nathorst emended by Srinivasan (1995) in its segmented shoot bearing a simple spiral of leaves, smooth cylindrical internode, and guard cells sunken below ring of subsidiary cells.

Among the species of *Pseudofrenelopsis* previously described, the European *P. varians* (Fontaine) Watson and American *P. parceramosa* (Fontaine) Watson differ from *P. glabra* in possessing an extremely thick cuticle and having trichomes on the adaxial surface of the leaf cuticle (Watson, 1977).

Although various species of *Pseudofrenelopsis* have been reported from China, most are provided with brief descriptions (Zhou, 1995). Recently, Zhou (1995) reexamined and combined the Chinese *Pseudofrenelopsis* into the following three species: *P. papillosa* (Chow et Tsao) Zhou, *P. dalatzensis* (Chow et Tsao) Zhou, and *P. heishanensis* Zhou (Table 1). *Pseudofrenelopsis glabra* is similar to these Chinese species in possessing a thinner internode cuticle than the European and American species. *Pseudofrenelopsis dalatzensis* and *P. heishanensis* can be distinguished from *P. glabra* by the stellate rim of the stomatal pit and absence of hairs on their leaf margins.

The shape of the cells, smooth periclinal walls, and thin anticlinal walls of the hypodermis of *Pseudofrenelopsis glabra* (Figures 3G, E) are very similar to the "epidermal cells" of *Pseudofrenelopsis heishanensis* described by Zhou (1995). However, detailed light and SEM microscopy of *P. heishanensis* is required prior to meaningful comparison of *P. heishanensis* and *P. glabra*.

Pseudofrenelopsis papillosa, redescribed in detail by Zhou (1995), possesses the most similar cuticle to that of *P. glabra* in having hairs on the margin of the leaf, round stomatal pits, and a thin cuticle. These resemblances may indicate a close phylogenetic relationship between these two species. *Pseudofrenelopsis glabra* is however, clearly distinguished from *P. papillosa* by a smaller number of subsidiary cells and absence of trichomes on the outer surface of the leaf adaxial cuticle.

Paleophytogeography.—Since Kimura (1961, 1975) has divided the Late Jurassic–Early Cretaceous floras of Japan and its adjacent areas into the Ryoseki-type and the Tetori-type floras, this paleophytogeographical distinction has been extended to East Asia with some modification, and the Mixed-type flora that consist predominantly of the Ryoseki-type element and subordinate Tetori-type element was added (Kimura, 1980, 1987; Kimura and Ohana, 1992; Cao, 1994; Ohana and Kimura, 1995).

Although the Mesozoic flora of Hokkaido is famous for its well preserved permineralized materials, the stratigraphic range of these materials is restricted to the Upper Cretaceous (Nishida, 1991). So far, the absence of Jurassic and Lower Cretaceous fossil plants from Hokkaido had prevented comparison of the Early Cretaceous flora of Hokkaido with the Ryoseki- and the Tetori-type floras.

Recently, Saiki (1997) described *Frenelopsis pombetsuensis*, from the Lower Cretaceous Yezo Group (Albian) of Hokkaido. The family Cheirolepidiaceae is a diagnostic taxon of the Ryoseki-type element reported only from the Ryoseki- and the Mixed-type floras (Ohana and Kimura, 1995). Thus, *Pseudofrenelopsis glabra* is the second evidence of the presence of Ryoseki-type element from Hokkaido.

Ohana and Kimura (1995) estimated that the Ryoseki-type floras flourished under tropical or subtropical conditions with an annual long arid season. Their idea is consistent with the thermophilous nature of frenelopsids proposed by Alvin (1982) based on the distribution of frenelopsids of the world and their possession of a thick cuticle. However, the two frenelopsids species from Hokkaido lack two of the xeromorphic features observed in many other frenelopsids, namely, a thick cuticle and trichomes on the internode surface. The cuticle thickness of eight species listed in Alvin (1982) are 8–110 μm thick in their periclinal wall rather than 3 μm and 3–4 μm thick as in *Frenelopsis pombetsuensis* and *Pseudofrenelopsis glabra* respectively. The cuticular features of *Frenelopsis pombetsuensis* and *Pseudofrenelopsis glabra* may reflect the rather humid condition inferred for the Albian of Pombetsu, rather than the xeric conditions from other regions of the world where frenelopsids were distributed (Alvin, 1982). This assumption is consistent with recent palynological data indicating that the group inhabited a variety of ecological niches (Watson, 1988).

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The first record of *Mesoturrilites* (Ammonoidea) from Hokkaido (Studies of the Cretaceous ammonites from Hokkaido and Sakhalin — LXXXIII)

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Abstract. Several small specimens collected years ago by A.I. from a locality in the Soeushinai area of Hokkaido are now identified as *Mesoturrilites boerssumensis* (Schlüter, 1876). The species has been reported from the Lower Cenomanian of western and central Europe and western Asia. Our material is also referred to the Lower Cenomanian on the biostratigraphic evidence. This may be the first record of *Mesoturrilites* in the northern Pacific region.

Key words : Cenomanian, geographic distribution, Hokkaido, *Mesoturrilites*, Pacific region, Turrilitidae

Introduction

A number of species belonging to *Mariella*, *Pseud-helicoceras*, *Ostlingoceras*, *Neostlingoceras*, *Turrilites* and *Hypoturrilites* of the family Turrilitidae [Ammonoidea] show worldwide distribution. Some of them occur fairly commonly in the Upper Albian and Cenomanian strata in Japan, although many of them are waiting for complete descriptions. In this paper a species of *Mesoturrilites* from Hokkaido is described.

Stratigraphic setting

The area concerned, called “Soeushinai”, was geologically mapped by Hashimoto *et al.* (1965) and has been recently reinvestigated by Nishida *et al.* (1996, 1997, 1998a, b). According to these authors, a thick series of strata called the Middle Yezo Subgroup of late Albian through Turonian age, is extensively exposed in this area. The subgroup is subdivided into Members My1 to My8 in a revised scheme of Nishida *et al.* (1996, fig. 10). The specimens described below were contained in a transported nodule obtained by A.I. in 1959. That nodule was collected in the upper reaches of the Sanjussen-zawa, a tributary of the River Uryu. The nodule is interpreted as a derivative from Member My3. This member consists primarily of mudstones which have sometimes fine-grained sands or sandy laminae and contain commonly calcareous nodules. Ammonoids occur fairly abundantly in Member My3 together with inoceramids and other mollusks. Some of them were described by Matsumoto and Inoma (1975, 1991) and Inoma (1980) and also amply listed by Nishida *et al.* (1996, 1997). The fauna forms the Assemblage Zone of *Graysonites adkinsi*, indicating the lower part of the Lower Cenomanian.

The overlying Member My4 is composed of ill-sorted conglomerates in some parts and predominant sandstones with some mudstones and conglomerates in other parts. It is poor in fossils. The succeeding Member My5 consists mainly of mudstones which contain numerous inoceramids with some associated ammonoids, representing the rest of the Cenomanian.

The Inoma's locality, numbered AI-72803, is concisely indicated in a map by Matsumoto and Inoma (1975, fig. 2) and more precisely in Figure 1. A fossiliferous nodule contains small specimens of *Algericeras proratum* (Coquand) and *Euhystrioceras* cf. *nicaisei* (Coquand) besides those of *Mesoturrilites* described herein. At another locality, R7239p, about 70m NEE of AI-72803, Y. Kawashita and N. Egashira obtained another ammonite which is identified by T.M. with *Gabbioceras yezoense* Shigeta. The three ammonite species indicate an early Cenomanian age and the mudstones around the above localities are referable to Member My3. Incidentally, as a result of Y. Inoue's examination of foraminifera, the strata exposed in the source area of the Sanjussen-zawa, including localities R7238, R7231, R7232, R7233 and R7234, have proved to be Member My5 (middle to upper part of the Cenomanian) (for details see Nishida *et al.*, 1998a). The two members My3 and My5 are probably in fault contact (Figure 1).

Repository

The specimens described below have numbers with the prefix TKD, which is the abbreviation of “Tokyo Kyoiku Daigaku [Tokyo University of Education]”, where A.I. was a student. Since this university was closed, A.I.'s collection of ammonoids from the Soeushinai area under TKD numbers has been temporarily stored in the Department of Geology,

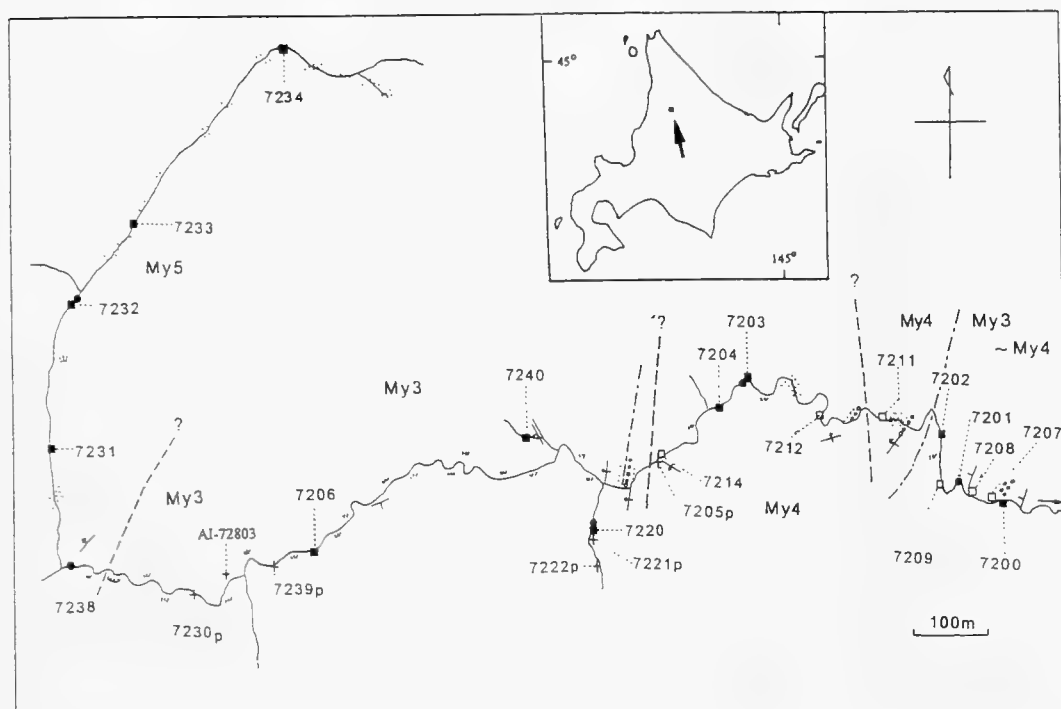


Figure 1. Route map along the upper course of the Sanjussen-zawa, cited from Nishida *et al.*, 1998a by permission. Inset is a map of Hokkaido in which the Soeushinai area is indicated by an arrow. Small solid circle: megafossil (in situ), cross: ditto (transported nodule), solid square: microfossil sample, empty square: rock sample, tiny empty circle: conglomerate, dots: sandstone, grass: no outcrop, blank along the route: mudstone, broken line: fault (inferred), chain: boundary of lithostratigraphic units (members). All the locality numbers should have prefix R, except for AI-72803.

Kyushu University in Fukuoka, but they should be eventually returned to the Department of Geosciences, Tsukuba University, Tsukuba, 305-0006 Japan, which is the new guise of the TKD.

Morphological terms

For the morphological terms used to describe the turritid ammonoids, we follow those of Wright and Kennedy (1996). Setting the apex of the turritid shell at the top, the terms upper and lower or adapical and adapertural [=adoral] are defined and the rows of tubercles or ribs on the face of each whorl are described in descending order as the first, the second and so on.

Palaeontological description

Order Ammonoidea Zittel, 1884
Suborder Ancyloceratina, Wiedmann, 1966
Family Turritidae Gill, 1871
Genus *Mesoturritiles* Breistroffer, 1953

Type species.—*Turritiles aumalensis* Coquand (1862, p. 323, pl. 35, fig. 5), by original designation of Breistroffer (1953, p. 1351).

Diagnosis.—Turritid ammonoid with four rows of tubercles

or ribs; the upper row made up of ribs or rounded tubercles, the second and the third rows spirally elongated tubercles on semicontinuous, narrow ridges separated by a groove; the fourth row of weak tubercles at the outer edge of the lower whorl surface; faint ribs may be elongated from the fourth row of tubercles toward a narrow umbilicus.

Remarks.—The lectotype and paralectotypes of the type species have been photographically illustrated by Wright and Kennedy (1996, text-fig. 146A–G).

At present five species are known in *Mesoturritiles*. The distinction between species is based on the size of the apical angle, mode of ribbing and/or tuberculation, whorl shape etc. Atabekian (1985, p. 75) referred *Turritiles colcanapi* Boule, Lemoine and Thévenin, 1907 to *Mesoturritiles*. However, we agree with Spath (1937, p. 523) and also Wright and Kennedy (1996, p. 323) on their assignment of *T. colcanapi* to *Ostlingoceras*.

The phylogenetic origin of *Mesoturritiles* is uncertain, but it can likely be sought in some form of *Mariella*. A sulcate variety of *Mariella oehlerti* (Pervinquier) may be a candidate, as Pervinquier (1910, p. 55, pl. 5, fig. 17) has already mentioned its affinity to *Mesoturritiles aumalensis*. Wright and Kennedy (1996, p. 346) have suggested *Mariella bicarinata* (Kner) as another allied form.

The type species and some other species of *Mesoturritiles* have been recorded from the Lower Cenomanian of both the

Tethys and Boreal provinces.

***Mesoturrilites boerssumensis* (Schlüter, 1876)**

Figures 2 and 3

Turrilites boerssumensis Schlüter, 1876, p. 129, pl. 38, figs. 6, 7.

Turrilites (*Mesoturrilites*) *boerssumensis* Schlüter. Immel, 1979, p. 636, pl. 4, fig. 4; Hiss, 1982, p. 190, pl. 7, figs. 11, 12; Atabekian, 1985, p. 75, pl. 27, figs. 3, 4.

Mesoturrilites boerssumensis (Schlüter). Wright and Ken-

nedy, 1996, p. 347, pl. 105, figs. 4, 20 (with full synonymy); Lehmann, 1998, p. 36, pl. 5, fig. 5.

Lectotype.—The original of Schlüter, 1876, pl. 38, figs. 6, 7, from the Cenomanian Pläner near Börssum, Germany, by subsequent designation of Juignet and Kennedy (1976, p. 67).

Material.—Four specimens, TKD30089A (Figure 2-1), TKD30089B (Figure 2-2), TKD30089C (Figure 2-3; Figure 3) and TKD30089D (unillustrated). They were removed by A.I. from a transported nodule at locality AI-72803 in the upper reaches of the Sanjussen-zawa of the Soeushinai area, northwestern Hokkaido (Figure 1).

Description.—TKD30089A consists of four whorls with estimated tower height 23.3 mm, apical angle about 19°, height and diameter of the preserved last whorl 5.4 mm and 11.2 mm respectively. Other three are smaller than the above and incomplete, representing younger stages.

The main part of the exposed whorl face is flattened or slightly convex and the interwhorl junction is feebly impressed. The ornament is typical for *Mesoturrilites*. On the upper half of the exposed whorl face there are slightly prorsiradial ribs of moderate breadth and density (Figure 2-1). They number 21 per whorl at diameter of 11 mm in TKD30089A and 16 or 15 at diameter 7 or 6 mm in TKD30089B or TKD30089C. At about the middle of the whorl face the ribs terminate at tubercles of the first row. These tubercles are subrounded at the base and pointed at the top, as far as the test is well preserved. The tubercles of the second row are narrowly clavate and rest on a blunt spiral ridge. They correspond in number to the tubercles of the first row but are displaced adaperturally. The space between the first and the second rows of tubercles forms a smooth band and may appear to be slightly concave on the internal mould. The tubercles of the third row are narrowly clavate and aligned along the narrow ridge along the lower seam of the whorl. The narrow interspace between the second and the third rows of clavi is distinctly sulcate. As is shown by TKD30089A, the spiral groove between the second and third rows of semi-continuous ridges is immediately above the interwhorl junction in early growth stages, but later it is covered by the shell layer of the succeeding whorl (Figure 2-1). The tubercles of the fourth row are close to those of the third row, but they are aligned on the outer margin of the lower whorl face. Weak ribs run from them toward a narrow umbilicus, showing slightly rursiradial curvature (Figure 2-1c).

A septal suture of a young stage is exposed on the whorl face of TKD30089C. As is shown in Figure 3, the saddle E/L is much broader than L/U. The relative disposition of the tubercles with respect to the sutural elements in shown is the same figure.

Discussion.—The specimens described above are undoubtedly identified with *Mesoturrilites boerssumensis* (Schlüter, 1876), redefined by Wright and Kennedy (1996, p. 347). In view of the variation of the rib density with growth and between individuals, the 17 ribs to a whorl specified in Schlüter's (1876, p. 636) description may not be incorrect. Hiss (1982, p. 190) counted 20 ribs on an example from Westphalia. Wright and Kennedy (1996, p. 347) estimated

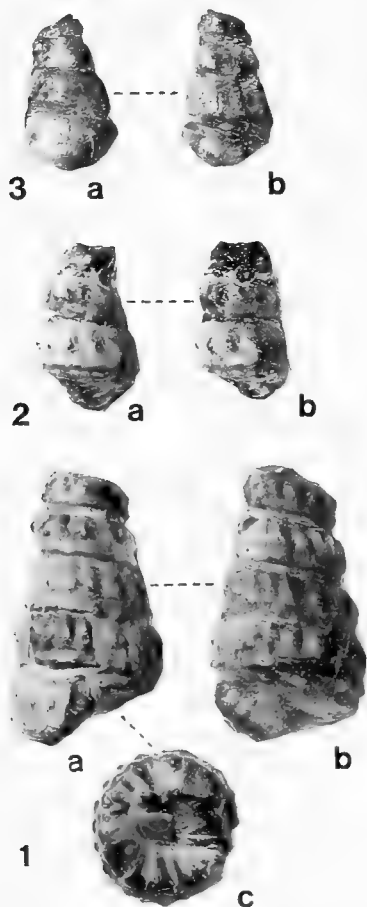


Figure 2. *Mesoturrilites boerssumensis* (Schlüter). 1. TKD30089A, two lateral (a, b) and basal (c) views. 2. TKD30089B, two lateral (a, b) views. 3. TKD30089C, two lateral (a, b) views. All $\times 2$.



Figure 3. *Mesoturrilites boerssumensis* (Schlüter). Suture of TKD30089C, showing relative position of the ribs and tubercles by dotted lines. Approximately $\times 8$.

as many as 24–26 ribs per whorl in a specimen from England, but 9 or 10 ribs are shown on its illustrated face of slightly less than half a whorl (*op. cit.*, pl. 105, fig. 4) as in our TKD30089A (Figure 2–1).

Hitherto described specimens, comprising those from Hokkaido, are more or less small, with diameters of the preserved last whorl less than 25 mm. The small size may be, therefore, a diagnostic character of this species. However, further investigation is required to search out a completely preserved specimen with a rostrate peristome and also to examine the problem of dimorphism.

Occurrence.—As for material. *M. boerssumensis* has been reported from the Lower Cenomanian of Germany (Westphalia and Bavaria), England, Poland and southern Turkmenistan (see synonymy list). Now its distribution is extended to Hokkaido. This may be the first record of *Mesoturrilites* from the northern Pacific region.

Acknowledgements

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Hokkaido 北海道, Sanjussen-zawa 三十線沢, Shumarinai 朱鞠内, Soeushinai 添牛内, Uryu 雨竜,
Yezo 蝦夷

Early Silurian actinocerid and orthocerid cephalopods from the Kerman area, East–Central Iran

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Abstract. Six species of uncoiled cephalopod, including the actinocerids *Actinoceratidae*, gen. and sp. indet., *Armenoceras banestanense* sp. nov., *A. sp.*, *Elrodoceras* sp. and *Huroniella iranica* sp. nov., and an orthocerid *Proteoceratidae*?, gen. and sp. indet., are present in collections made recently from an unnamed formation near Banestan village in the Kerman area of southern East–Central Iran. The cephalopod fauna contains forms closely related with those from Laurentia, and is considered to be of Early Silurian age. This discovery reveals that the geologic age of these cephalopod-bearing horizons should be revised from a vague late Ordovician or early Silurian one. These horizons are correlative with the Niur Formation in the Shirgesht area of northern East–Central Iran.

Key words : Actinocerida, cephalopods, Early Silurian, Iran, Orthocerida

Introduction and geologic setting

During the course of field work in February, 1996, several uncoiled cephalopods were discovered by two of us (Y.K. and D.W.) at three localities near Banestan village in the Kerman area of southern East–Central Iran (Figure 1). The purpose of this paper is to document the fauna and to discuss its implications. The specimens are deposited in the University Museum of the University of Tokyo (UMUT).

Until its separation and northward drifting at or near the Permian–Triassic boundary, the Iran terrane belonged to the Gondwana continent, and the Kerman area was part of a carbonate platform around the margin of Gondwana (e.g., Lensch *et al.*, 1984). The geology of the Kerman area has been described by Huckriede *et al.* (1962), Zohrenbakhsh and Vahdati Daneshmand (1992) and Richards *et al.* (1994). These investigations discerned three units in the Lower to Middle Paleozoic strata: Upper Cambrian to Lower Ordovician carbonates of the Mila Formation, the Arenig (upper Lower Ordovician) graptolite shale of the Katkoyeh Formation, and an unnamed formation probably ranging from Upper Ordovician to Middle Devonian that mainly consists of clastics with subordinate carbonates. The cephalopods described herein occur in argillaceous and/or bioclastic limestone of the unnamed formation (Figure 2). The cephalopod-bearing horizons have been described as “orthoceras limestone” by Huckriede *et al.* (1962), and regard-

ed as being of late Ordovician or early Silurian age. However, the exact biostratigraphic range of the cephalopod-bearing horizons has so far been a matter of debate.

Detailed analysis of morphologic features of the present cephalopods resulted in the identification of five Early Silurian actinocerid and one orthocerid species that provide insights into the precise age and paleobiogeographic affinities of the fauna. This is the first modern taxonomic treatment of Silurian cephalopods from the Iran terrane.

Systematic paleontology

Subclass Actinoceratoidea Teichert, 1933
Order Actinocerida Teichert, 1933
Family Actinoceratidae Saemann, 1853

Genus and species indeterminate

Figures 3–7, 5–5, 6

Discussion.—A single incomplete specimen of a gently cyrtoconic (?) phragmocone is assigned to the *Actinoceratidae*, genus and species indeterminate, based on its relatively long and normal cyrtocochanitic septal necks and the high ratio (at least 3.2) of maximum diameter/length of its siphuncular segments.

The restricted development of the annulosiphonate

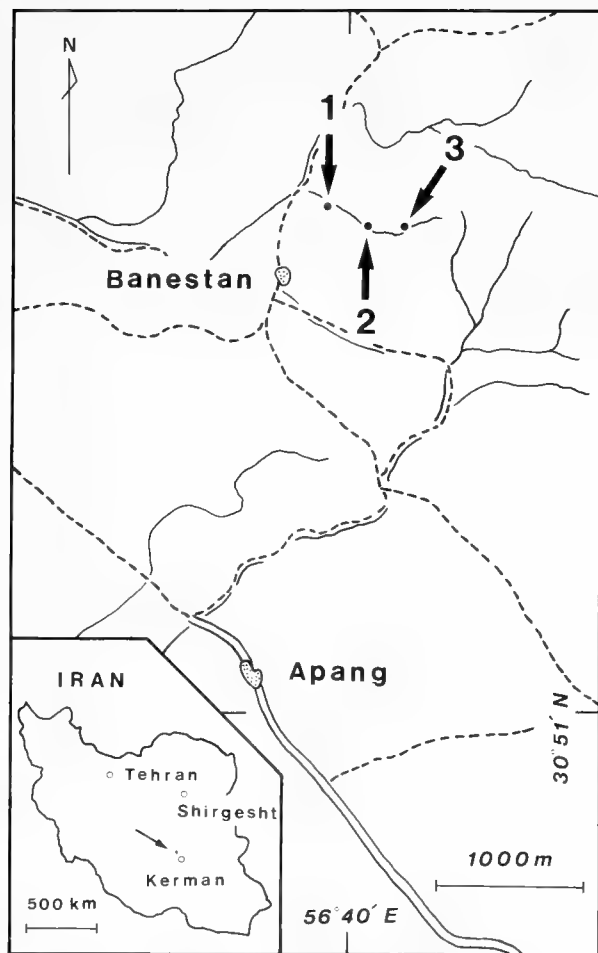


Figure 1. Index map of fossil localities (1-3) in the Kerman area (small arrow in inset), southern East-Central Iran.

deposits on the ventral siphuncular wall and the straight radial canals projecting to the vicinity of brims are an unusual diagnosis for the family and indicate a possibility that the species represents a new genus. Unfortunately the ventral shell is not preserved in the only specimen available. Until additional material is found, the present material is considered too poor to justify naming it to the generic level.

Material and occurrence.—UMUT PM 27332, 72 mm in length, from locality 3.

Family Armenoceratidae Troedsson, 1926
Genus *Armenoceras* Foerste, 1924a

Type species.—*Actinoceras hearsti* Parks, 1913.

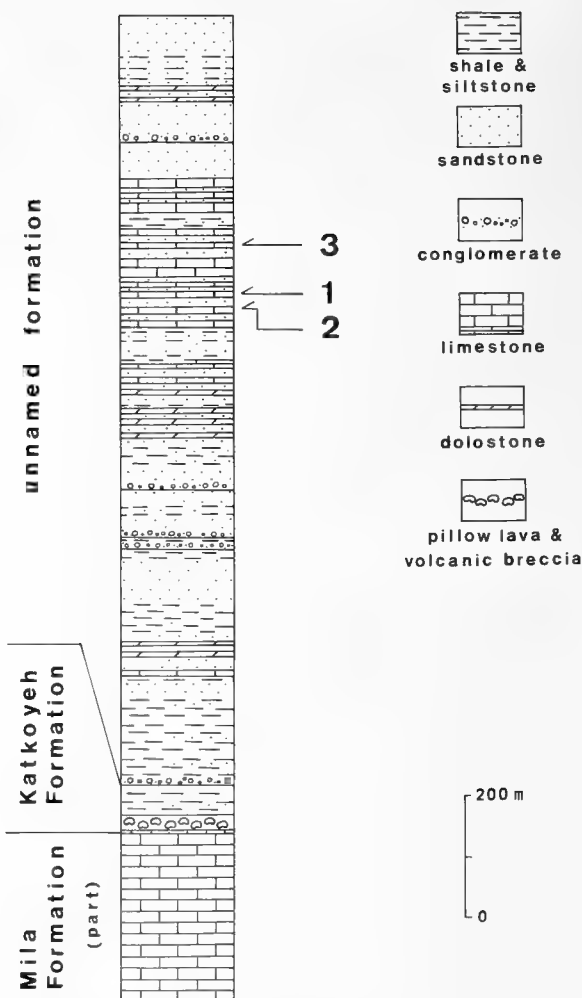


Figure 2. Generalized stratigraphic section of the Lower to Middle Paleozoic rocks near Banestan village in the Kerman area. Stratigraphic horizons of each locality are indicated.

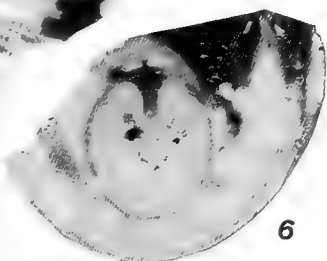
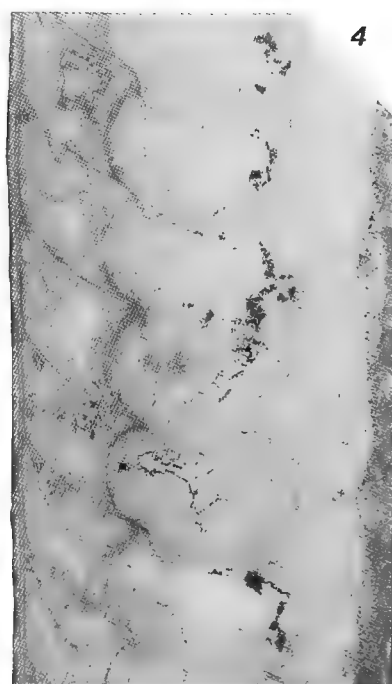
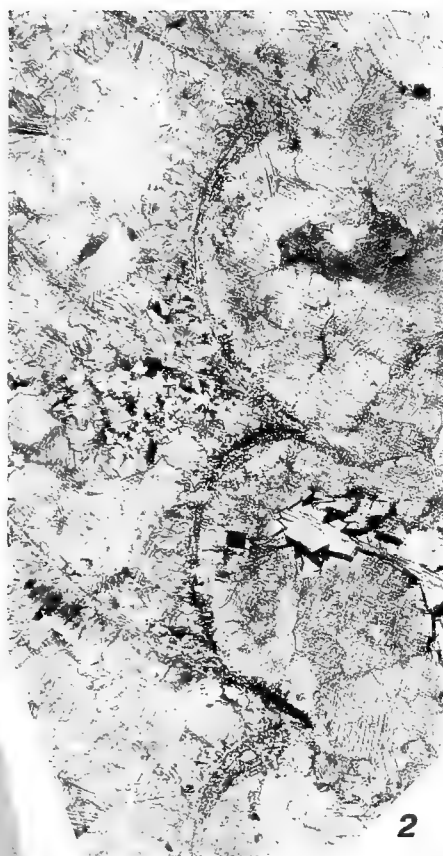
Armenoceras banestanense sp. nov.

Figures 3-1-6

Diagnosis.—*Armenoceras* with smaller ratio of maximum siphuncular diameter to shell diameter (approximately 0.3-0.4), very narrow adnation areas in dorsal siphuncular wall; cameral deposits well developed; central canal situated on dorsal margin.

Description.—Orthoconic shells with circular cross sections, moderate shell expansion for the genus, lacking

Figure 3. 1-6. *Armenoceras banestanense* sp. nov., 1-4, 6: holotype, UMUT PM 27328, 1, dorsoventral thin section, venter on left, $\times 2$, 2, dorsoventral thin section, showing details of ventral wall of siphuncle, $\times 14$, 3, dorsoventral thin section, showing details of dorsal wall of siphuncle, note very narrow adnation area, $\times 14$, 4, dorsoventral thin section, showing details of ventral shell, $\times 5$, 6, transverse thin section of adoral end, venter down, $\times 2$, 5: paratype, UMUT PM 27327, weathered surface of dorsal side, coated with ammonium chloride, $\times 2$. 7. Actinoceratidae, gen. and sp. indet., UMUT PM 27332, dorsoventral thin section, venter on right, $\times 2$.



conspicuous surface ornamentation; adoral end of imperfect phragmocone of holotype attains approximately 25 mm (slightly deformed) in diameter. Septa closely spaced, moderately shallow; siphuncle large, ratio of maximum siphuncular diameter to shell diameter is small for genus, approximately 0.3–0.4, submarginal in position; septal necks very short, 0.15–0.21 mm in length, strongly recurved cyrtchoanitic; brims short for genus, 0.44 mm in well preserved dorsal brim of holotype, in contact with apical surface of septa; diameter of septal foramen 5.9–8.9 mm in holotype; connecting rings broadly expanded; adnation areas moderate to relatively narrow (their length in dorsoventral section approximately 0.9 mm) in ventral siphuncular wall, and very narrow (*do.* approximately 0.3 mm) in dorsal siphuncular wall; maximum diameter/length ratio of siphuncular segments 3.5–4.0. Cameral deposits well developed, episeptal-mural and forming circumsiphuncular ridges, additional hyposeptal deposits recognized in ventral side of camerae; ventral endosiphuncular deposits fusing to form thick lining on siphuncular wall, differentiated into outer annuli and inner lining deposits; profile of outer annuli laterally elongated elliptical in longitudinal section; development of endosiphuncular deposits on dorsal siphuncular wall weak, separated annuli with semicircular profile in longitudinal section. Central canal situated on dorsal margin, branching off narrow radial canals, of which distal parts are curved adorally; perispatia small, situated near adoral end of each connecting ring.

Discussion.—*Armenoceras banestanense* sp. nov. is most similar to *A. hearsti* (Parks, 1913; 1915, pl. 6, fig. 5; Foerste, 1924a, pl. 13, fig. 4) which has a siphuncular position and a form ratio of the siphuncular segments like the new species. *Armenoceras hearsti* was reported from "Limestone Rapids" on the Severn River, Ontario, Canada, and derived from the Ekwan River or Attawapiskat Formation of late Llandovery (Early Silurian) age (Jin et al., 1993). However the former is distinguishable from the latter by its smaller siphuncle (ratio of maximum siphuncular diameter to shell diameter approximately 0.45 in *A. hearsti* versus 0.3–0.4 in *A. banestanense*), its somewhat weaker inflation of the connecting rings with the narrower adnation area, and the marginal position of its central canal.

The brims of *Armenoceras banestanense* and the cooccurring *A. sp.* (this report) are frequently missing or obscured by diagenesis, thus they are apt to be incorrectly described as "achoanitic".

Material and occurrence.—Holotype, UMUT PM 27328, an incomplete phragmocone, 51 mm in length; paratype, UMUT PM 27327, an incomplete phragmocone, 42 mm in length. Both from locality 3.

Etymology.—The specific name is derived from the village

named Banestan near the type locality.

Armenoceras sp.

Figures 4–5, 7, 8

Description.—Orthoconic shells with gradual shell expansion, shell diameter reaches 20 mm at adoral end of largest specimen (UMUT PM 27329). Siphuncle subcentral in position, consisting of strongly recurved cyrtchoanitic septal necks and expanded connecting rings with relatively wide adnation area; brims in contact with septa; maximum diameter/length ratio of siphuncular segments approximately 2.5. Cameral deposits episeptal-mural and hyposeptal; endosiphuncular deposits of annuli have elliptical profile in longitudinal section. Nearly straight radial canals connect with prespatia in apical shell.

Discussion.—This species is easily distinguished from *Armenoceras banestanense* sp. nov. by its subcentral siphuncular position and the smaller form ratio of the siphuncular segments.

Material and occurrence.—Two incomplete phragmocones, UMUT PM 27329, 62 mm in length, and 27330, 61 mm in length, from locality 3.

Genus *Elrodoceras* Foerste, 1924b

Type species.—*Cyrtoceras indianense* Miller, 1892.

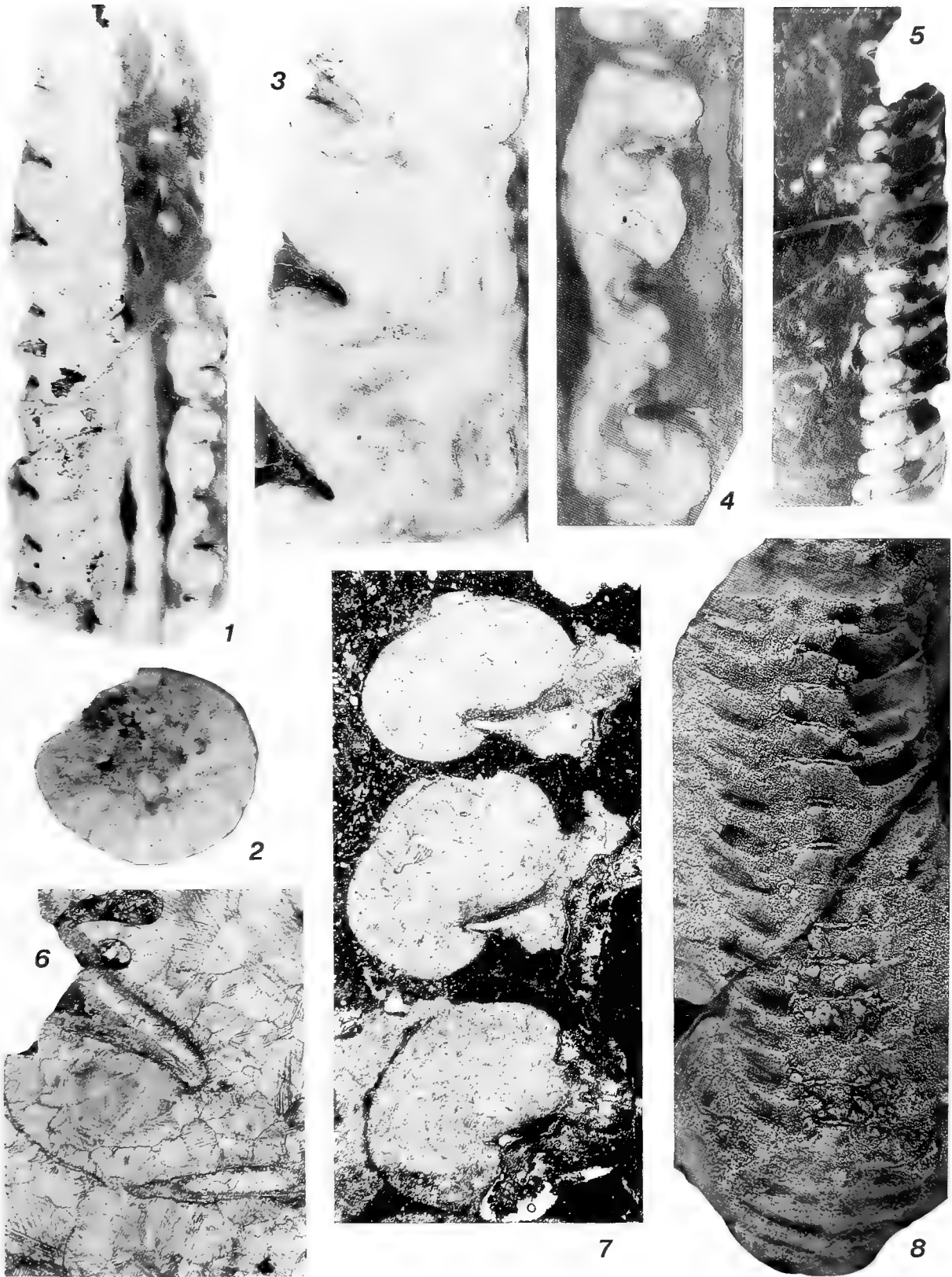
Elrodoceras sp.

Figures 5–1–3

Description.—Siphuncle gently curved (?) and large, attains at least 15.5 mm in maximum diameter, with relatively low ratio of maximum diameter/length in siphuncular segment for armenoceratids, at approximately 2.5–2.7; siphuncular position submarginal (?). Septal necks bend adapically, thus septal foramen is funnel-shaped; brims strongly recurved cyrtchoanitic, in contact with septa; connecting rings form very wide adnation area and moderately inflated free parts. Cameral deposits episeptal-mural and hyposeptal; endosiphuncular deposits well developed, annulosiphonate. Central canal surrounded by lining deposits that are darker in color than annulosiphonate deposits; radial canal arched with branches.

Discussion.—Except for the deposit-filled siphuncle, the shell of this only known specimen is broken and weathered on the dorsum, thus accurate shell shape and siphuncular position can not be determined in the present material. Nevertheless, this species appears most similar to *Elrodoceras* in its siphuncular morphology such as the funnel-shaped

Figure 4. 1–4, 6. *Huroniella iranica* sp. nov., holotype, UMUT PM 27326, isolated siphuncle, 1, dorsoventral thin section, venter on left, $\times 2$, 2, transverse thin section of apical end, venter down, $\times 2$, 3, dorsoventral thin section, showing details of ventral wall of siphuncle, $\times 5$, 4, dorsoventral thin section, showing details of dorsal wall of siphuncle, $\times 5$, 6, dorsoventral thin section, showing details of septal neck and radial canal in ventral wall of siphuncle, note contact layer and depression on apical surface of septum, $\times 14$. 5, 7, 8. *Armenoceras* sp., 5, 7: UMUT PM 27330, 5, dorsoventral thin section, venter on right, $\times 2$, 7, dorsoventral thin section, showing details of ventral wall of siphuncle, $\times 14$, 8: UMUT PM 27329, weathered surface of ventral side, coated with ammonium chloride, $\times 2$.



septal foramen, arched radial canals and relatively low form ratio of the siphuncular segments.

Material and occurrence.—UMUT PM 27331, 55 mm in length, from locality 3.

Family Huroniidae Foerste and Teichert, 1930

Genus *Huroniella* Foerste, 1924a

Type species.—*Huronia inflecta* Parks, 1915.

Huroniella iranica sp. nov.

Figures 4-1-4, 6

Diagnosis.—*Huroniella* with asymmetrical connecting rings; siphuncular segments short; adoral bending of septa lacking; width of septal foramen/distance of neighboring septal necks 2.3-3.0; perispatia wide, attain distal end of brim.

Description.—Large straight siphuncle, 20.5 mm in lateral diameter of apical end of holotype; septal necks short, approximately 0.5 mm in length, strongly recurved cyrtchoanitic; brims 0.63-0.68 mm in length, in contact with apical surface of septa; diameter of septal foramen 12.5-14.0 mm; shape of connecting rings asymmetrical in dorsoventral section, ventral connecting rings strongly inflated, bluntly pointed arcs with obliquely adoral direction in longitudinal section; adnation area in adoral surface of septa very wide, forming contact layer by thickening of connecting ring; in contrast to adoral surface of septa, relatively narrow in apical surface, contact layer also recognized where septa are weakly depressed; dorsal connecting rings semicircular with narrow adnation area lacking evident contact layer; siphuncular segments short for huroniids, width of septal foramen/distance of neighboring septal necks 2.3-3.0. Endosiphuncular deposits of annuli well developed leaving large central canal in a position slightly shifted from axis; radial canals curving adapically and branching, to join wide perispatia, which attain distal end of brim.

Discussion.—*Huroniella iranica* sp. nov. appears to be most like *H. persiphonata* (Billings, 1857; Foerste, 1927, pl. 44, fig. 1; Teichert, 1933, figs. 4, 20) from the upper Llandovery Jupiter Formation of Anticosti Island, Canada. The Laurentian species shares the asymmetrical profile of its connecting rings with the present new species. The most obvious difference between these species is the septal morphology, i.e., a strong adoral bending of the septum is recognized in *Huroniella persiphonata*, but only a weak depression on the adoral septal surface is representative of *H. iranica*. In addition, the width of septal foramen/distance of neighboring septal necks ratio (approximately 2 in *H.*

persiphonata versus 2.3-3.0 in *H. iranica*) is also a diagnostic feature.

Huroniella inflecta (Parks, 1915, pl. 6, fig. 4; Foerste, 1924a, pl. 16, figs. 2a, b; Teichert, 1933, fig. 12), known from the "Limestone Rapids" in Ontario, is distinguished from the present species by having more strongly inflated dorsal connecting rings with a nearly symmetrical profile in dorsoventral section.

Material and occurrence.—Holotype, UMUT PM 27326, an isolated and incomplete siphuncle 65 mm in length, from locality 1.

Etymology.—The specific name is derived from Iran.

Subclass Nautiloidea Agassiz, 1847

Order Orthocerida Kuhn, 1940

Superfamily Pseudorthocerataceae Flower and Caster, 1935

? Family Proteoceratidae Flower, 1962

Genus and species indeterminate

Figures 5-4, 7

Discussion.—The poorly preserved specimen consists of a gradually expanding orthoconic shell with relatively short camerae, subcentral siphuncle consisting of short cyrtchoanitic septal necks and inflated connecting rings. Its maximum diameter/length ratio of siphuncular segments is approximately 1.5, and cameral deposits are episepal.

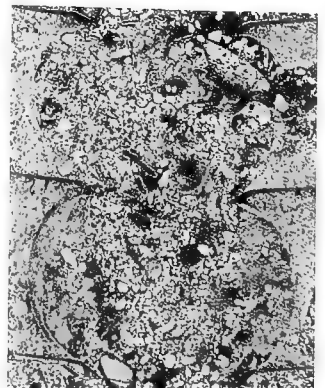
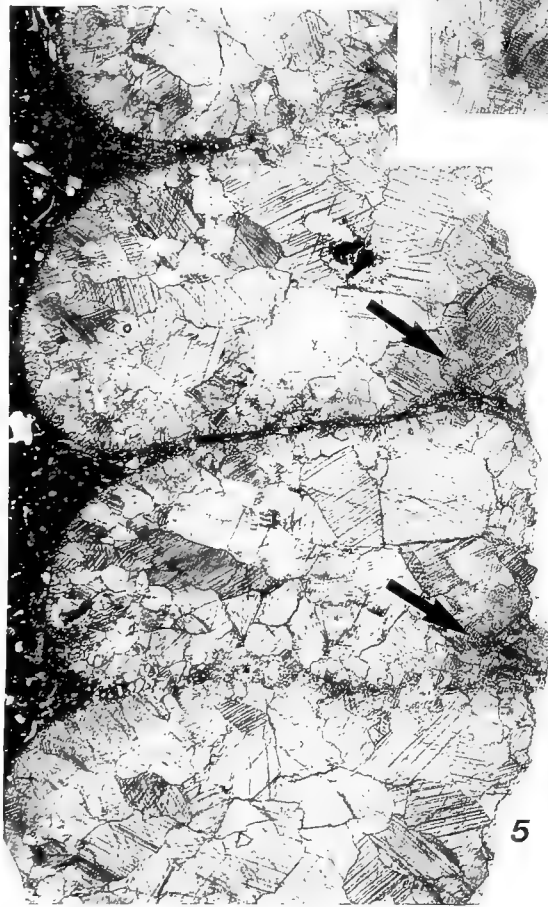
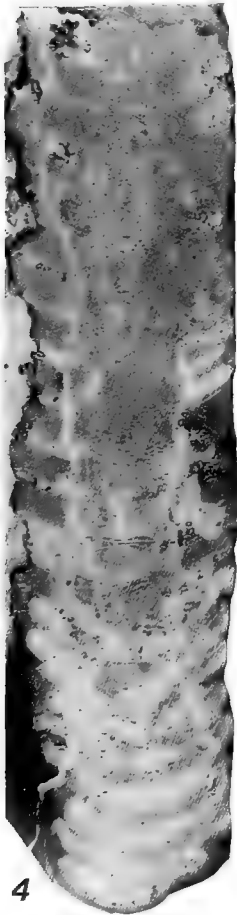
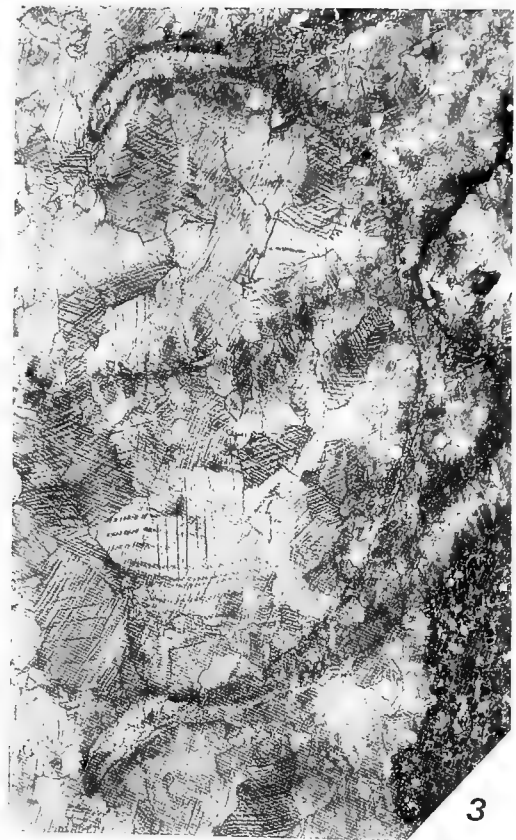
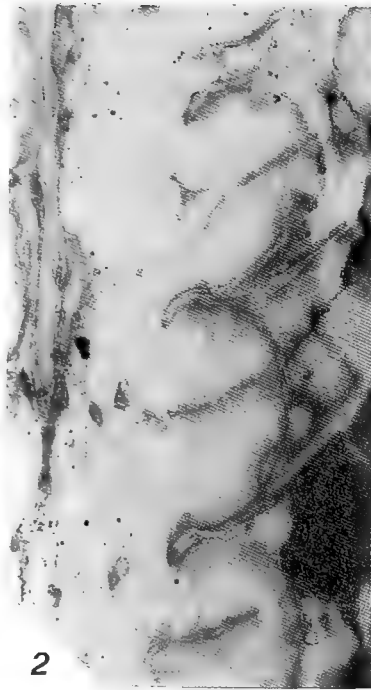
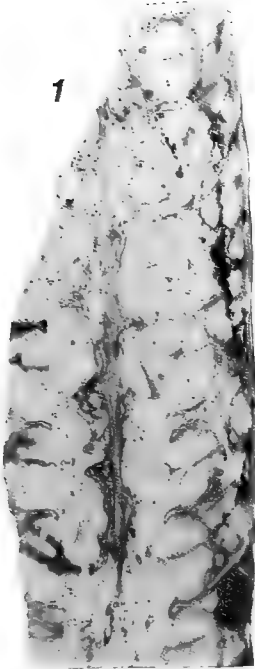
This species probably belongs to the Proteoceratidae, and its large siphuncular segment ratio for an orthoceras suggests a possible relationship with *Ephippiorthoceras*, although the material is insufficiently preserved to identify any further.

Material and occurrence.—Single incomplete phragmocone, UMUT PM 27333, 74 mm in length, from locality 2.

Stratigraphic and paleobiogeographic implications

The cephalopod species recognized at each locality are as follows: locality 1, *Huroniella iranica* sp. nov.; locality 2, Proteoceratidae?, gen. and sp. indet.; and locality 3, Actinoceratidae, gen. and sp. indet., *Armenoceras banestanense* sp. nov., *A. sp.*, and *Elrodoceras* sp. The most useful taxon for correlation is *Huroniella*, whose range is known with certainty from late Llandovery to early Wenlock strata in Laurentia and Baltica. Species similar to *Huroniella iranica* are found in the Anticosti Island and Hudson Bay areas and are of late Llandovery age. *Elrodoceras* is the only Silurian cephalopod previously known from Laurentia, Avalonia, Baltica and Siberia. *Armenoceras banestanense* sp. nov. is related to the late Llandovery species *A. hearsti* from the Hudson Bay area, and the genus is cosmopolitan.

Figure 5. 1-3. *Elrodoceras* sp., UMUT PM 27331, 1, dorsoventral thin section, venter on right, $\times 2$, 2, dorsoventral thin section, showing details of ventral wall of siphuncle, $\times 5$, 3, dorsoventral thin section, showing details of septal necks, radial canal and connecting ring in ventral wall of siphuncle, note adapical bending of septal necks, $\times 14$. 4, 7. Proteoceratidae?, gen. and sp. indet., UMUT PM 27333, 4, longitudinal thin section, $\times 2$, 7, longitudinal thin section, showing details of siphuncle, $\times 8$. 5, 6. Actinoceratidae, gen. and sp. indet., UMUT PM 27332, 5, dorsoventral thin section, showing details of ventral wall of siphuncle, arrows indicate septal necks, $\times 14$, 6, dorsoventral thin section, showing details of dorsal wall of siphuncle, $\times 14$.



and ranges from Middle Ordovician to Late Silurian in age. Besides cephalopods, the Wenlockian bryozoan species *Trematopora beikhemensis* is identified by S. Sakagami (personal communication) from locality 1. Although locality 2 lacks a clear age indicator, lithologically the three horizons may belong to a stratigraphic unit without notable breaks. On the basis of this evidence, we infer that at least the cephalopod-bearing horizons in the unnamed formation indicate a late Llandovery (or early Wenlock) age, and are lithologically and chronostratigraphically correlative with the Niur Formation (Ruttner *et al.*, 1968) in the Shirgesht area of northern East-Central Iran. On the other hand, the affinity of the cephalopod fauna is apparently with northeastern Laurentia. This new material suggests a faunal connection between Gondwana and Laurentia during Early Silurian times.

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Occurrence of Carboniferous corals from the Geumcheon Formation of Danyang area, Korea

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Abstract. Two species of Carboniferous coral, *Arachnastraea manchurica* and *Diphyphyllum delicatum*, are described for the first time from the upper part of the Geumcheon Formation of the Danyang area, Korea. They were previously reported as Devonian corals, *Disphyllum* sp. and *Phillipsastraea* sp. Associated fossils are fusulinids, including *Beedeina schellwieni*, *B. siviniensis*, *B. samarica*, *B. sp.*, *Fusulina cylindrica*, *F. sp.*, *Fusulinella mosquensis*, *Fusulinella provecta*, *Neostaffella sphaeroidea*, and *Ozawainella turgida*. Occurrence of these corals and fusulinids suggests that the upper part of the Geumcheon Formation is middle Moscovian in age.

Key words : Carboniferous, coral, Danyang area, Korea

Introduction

Yabe and Suzuki (1955) first reported specimens of corals from a limestone bed in Danyang area, Korea. They assigned them in open nomenclature to colonial corals of Devonian type as *Disphyllum* sp. and *Phillipsastraea* sp. and suggested that Devonian deposits existed in Danyang area. Unfortunately, their specimens were lost. Furthermore, they figured only one weathered surface and one polished-slab figure of *Disphyllum* sp. and offered no systematic descriptions.

On the basis of a second discovery of coral specimens of *Phacellophyllum* sp.? (*Disphyllum* sp.) associated with fusulinids including *Fusulina* sp., *Fusulinella* sp., and *Neostaffella* sp. from nearly the same horizon as that of Yabe and Suzuki (1955), Cheong (1972) saw a problem in the Danyang area, with a Devonian dating. He mentioned that the limestone containing the coral is not Devonian but Moscovian (Late Carboniferous) in age and surmised that this coral, which had been known as a Devonian type, probably survived into the Carboniferous.

Several months after Cheong's report, Kato (1972) reexamined the figures of Yabe and Suzuki (1955) and briefly documented that *Disphyllum* sp. and *Phillipsastraea* sp. reported from the Danyang area by Yabe and Suzuki (1955) are *Diphyphyllum* sp. and *Arachnastraea* sp. respectively.

Recently well preserved coral specimens, which are closely associated with abundant fusulinids, were discovered from a limestone bed of the Geumcheon Formation by the present authors. The purpose of this paper is to report an additional occurrence of Carboniferous coral specimens, which are described here as *Diphyphyllum delicatum* and *Arachnastraea*

manchurica, and to compare these with the Devonian corals *Disphyllum* sp. and *Phillipsastraea* sp. illustrated by Yabe and Suzuki (1955).

Geologic setting and fossil locality

General geological studies in the Danyang area have previously been carried out by many investigators (Kobatake, 1942 ; Brill, 1957 ; Lee and Kim, 1966 ; Son *et al.*, 1967 ; Park and Cheong, 1975 ; Park *et al.*, 1975 ; Kim, 1981). Kim (1971) studied the Paleozoic and Mesozoic paleocurrents of the Danyang Coalfield on the basis of sedimentary structures. Structural analysis and tectonic studies of the Danyang area have been recently carried out by Cho *et al.* (1986), Kim and Koh (1992), Kim *et al.* (1992a), Kim *et al.* (1992b), and Kim *et al.* (1994).

The Permo-Carboniferous sedimentary strata, the Pyeongan Supergroup, in southern Korea are widely distributed in the Danyang, Taebaeg, Yeongweol, Jeongseon, and Gangneung areas. The sediments are shallow marine to fluvial in origin and consist predominantly of sandstone and shale with small amounts of carbonate.

Cheong (1973) subdivided the Pyeongan Supergroup into the Carboniferous Manhang and Geumcheon formations, the Permian Bamchi, Jangseong, Hambaegsan, Dosagok and Kohan formations, and Triassic Donggo Formation in ascending order.

In Danyang area, the Carboniferous strata disconformably cover the Ordovician strata and are divided into two formations, namely, the Manhang and Geumcheon formations (Cheong, 1971) and are interunconformably overlain by the Jurassic deposits (Figure 1). Cheong (1971) firstly carried out

biostratigraphic research on fusulinids in the Danyang area and described 37 fusulinid species belonging to 11 genera.

The Carboniferous Manhang Formation unconformably

overlies the Ordovician strata. The formation, about 175 m thick, is characterized by red to purple shale and greenish coarse sandstone, with the intercalation of nine white and

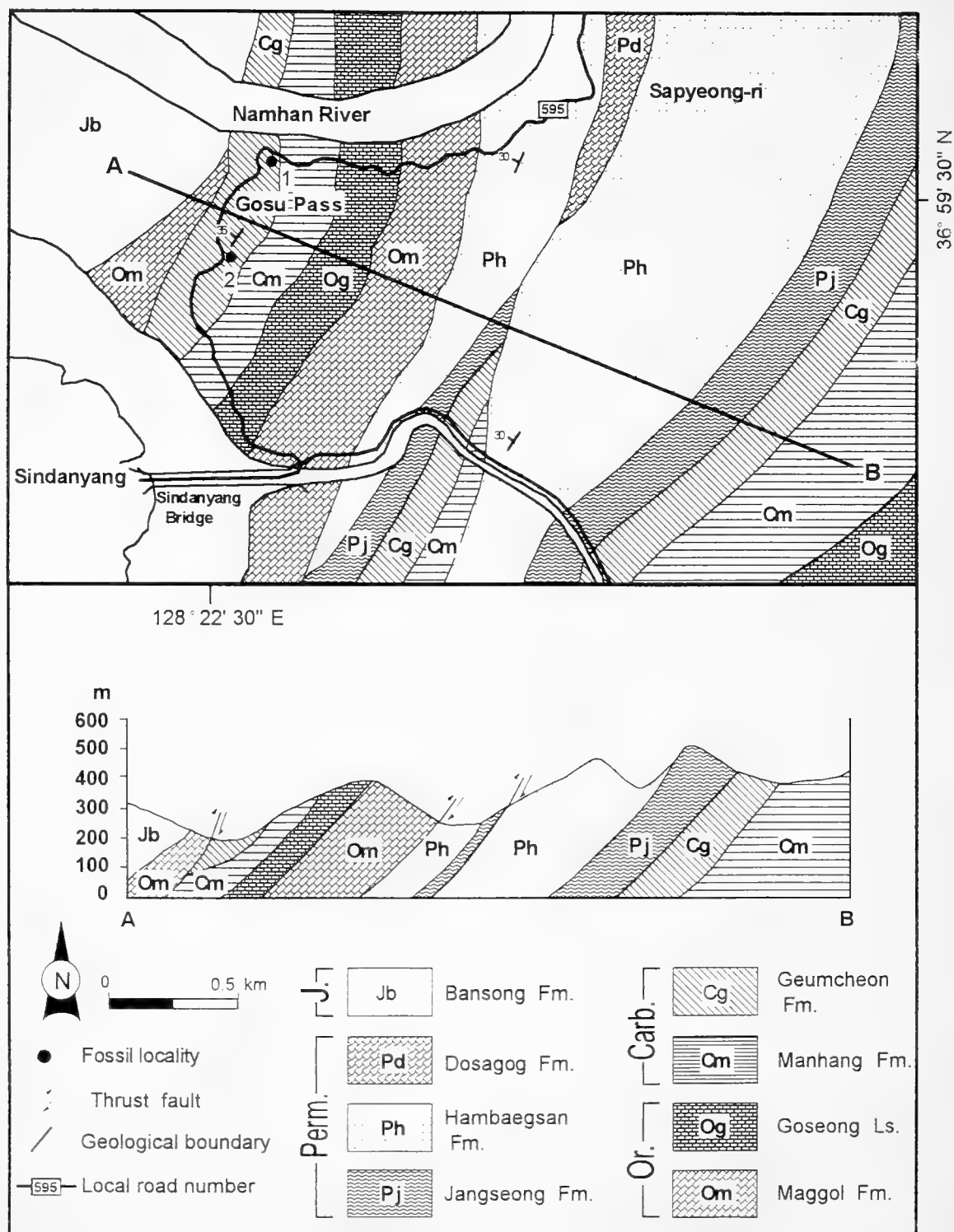


Figure 1. Geological map and fossil localities of study area. (After Son *et al.*, 1967 ; Lee and Kim, 1995)

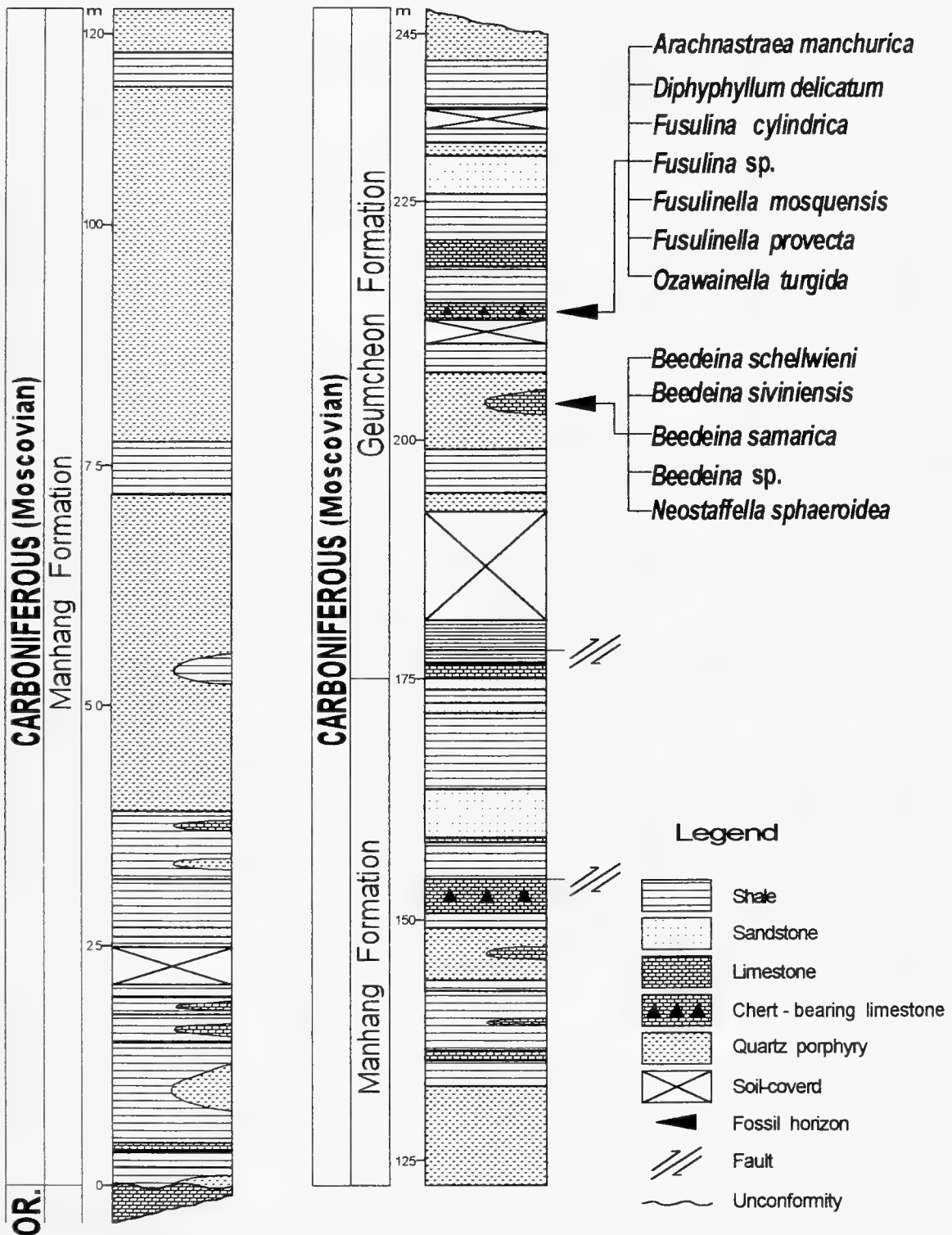
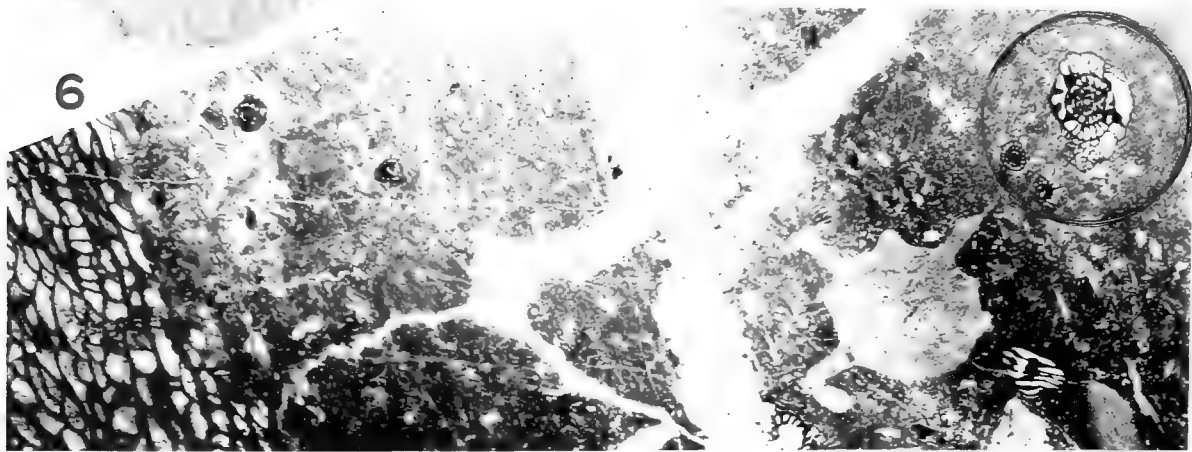
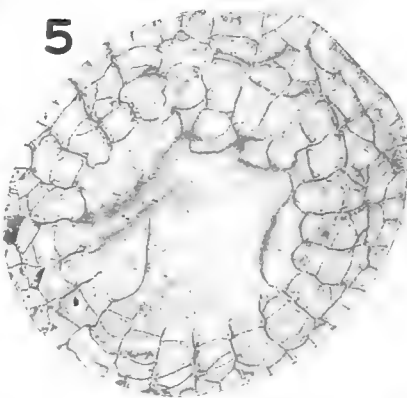
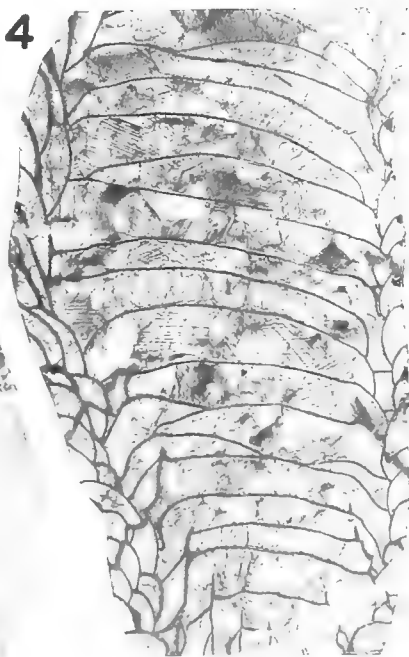
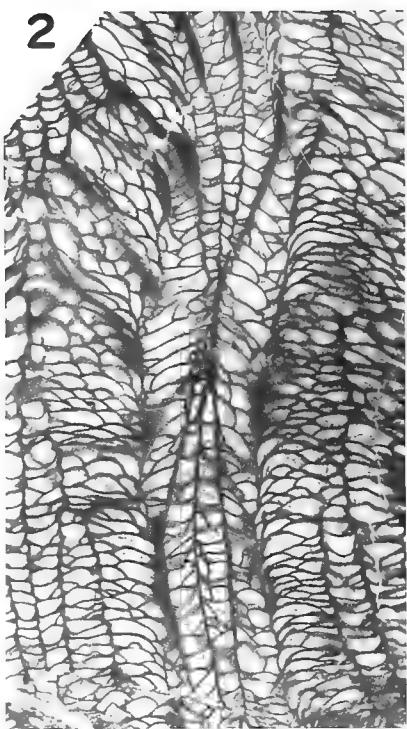
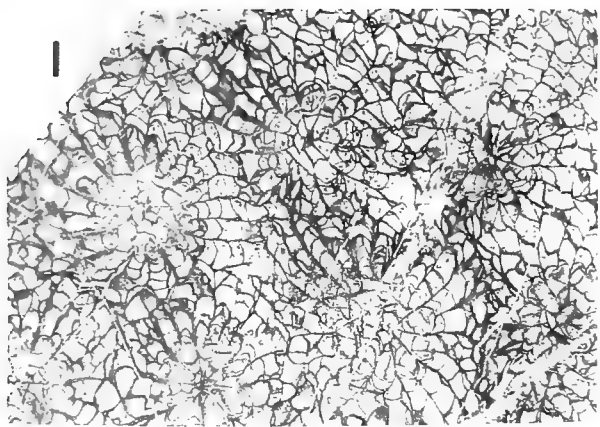


Figure 2. Measured stratigraphic section of study area.

light gray limestone beds or lenses in the measured section (Figure 2). In the upper part, the formation contains gray to bluish-gray limestone which bears white chert.

The Geumcheon Formation from which the coral specimens were collected is about 70 m thick and conformably covers the Manhang Formation. The formation comprises a



variety of terrigenous sediments intercalated with dark gray limestone lenses (Figure 2). The upper part of the formation is characterized by black shale and greenish sandstone. Abundant and diverse corals and fusulinids were only recorded from the limestone units in the formation. Lee and Kim (1995) also described *Beedeina schellwieni*, *Fusulina* sp., *Neostaffella sphaeroidea*, and *Ozawainella turgida* from the Geumcheon Formation near Gosu Pass in the Danyang area.

All of the specimens considered here were collected from a measured section of the Geumcheon Formation exposed in Gosu Pass along the local road 595, Danyang area (Figure 1). The fossil locality 1 is exposed near the top of Gosu Pass, about 1.2 km north of the Sindanyang Bridge. The limestone bed of locality 1, which is 2 m in thickness, is composed of abundant fusulinids and coral fragments which can not be used in the description. Many kinds of bioclasts, foraminifera, conodonts, brachiopods, and crinoids, were also found from the limestone bed.

The fossil locality 2 is about 800 m northwest from the Sindanyang Bridge. Fossil specimens were collected from a 5 m thick chert-bearing limestone bed which is stratigraphically nearly 40 m above the base of the Geumcheon Formation. The limestone is characterized by gray to dark gray color (Figure 2). Abundant corals together with fusulinids, brachiopods, bryozoa, and crinoid stems are clearly shown on the weathered surface of limestone bed.

Systematic description

The conventional treatment has been followed in the taxonomic hierarchy above the species level. The morphologic terminology used for systematic description followed is that of Hill (1935, 1956, 1981), the terminology of microstructural elements is that of Kato (1963, 1968). Specimens collected for the present study and described herein are housed in the Department of Earth Science Education, Korea National University of Education.

Phylum Cnidaria Hatschek, 1888

Class Anthozoa Ehrenberg, 1834

Order Rugosa Milne-Edwards and Haime, 1850

Suborder Streptelasmatina Wedekind, 1927

Family Lithostrotionidae d'Orbigny, 1851

Genus *Arachnastraea* Yabe and Hayasaka, 1916

Arachnastraea Yabe and Hayasaka, 1916, p. 69.

Type species.—*Arachnastraea manchurica* Yabe and Hayasaka, 1916, from the Lower Permian of South Manchuria.

Diagnosis.—Corallum compound, massive, typically cerioid or astraoid. Septa numerous, of two orders. Septa thin, usually extending across tabularium to columella but partly

discontinuous in dissepimentarium. Both major and minor septa are well developed. Tabulae conical, complete or incomplete, regular dissepimentarium (slightly modified after Hill, 1956).

Remarks.—In the typical species of the Devonian *Phillipsastraea* d'Orbigny, the septa never extend to the center of the corallites with horse-shoe dissepiments. The septa are dilated, especially at inner margin of dissepimentarium, and there is always a conspicuous inner wall formed by the abrupt thickening of all the septa. These characteristic features are not visible in *Arachnastraea* (Yabe and Hayasaka, 1916). Kato (1972) concluded that Yabe and Sugiyama (1940) misdescribed *Arachnastraea* as *Phillipsastraea* in an occurrence from Cheonseongri, Suncheongun, Pyeongan-namdo, Northwest Korea.

Arachnastraea manchurica Yabe and Hayasaka, 1916

Figures 3-1; 3-2

Arachnastraea manchurica Yabe and Hayasaka, 1916, p. 69.

Material.—KNUE 96201-96216 (KNUEDY Locality 2). Four specimens for this study were collected by the present authors from the measured stratigraphic section (see Figure 2).

Description.—*Transverse section description*: Corallum is astraoid and composed of nearly equal-sized polygonal corallites which are 4.1–6.6 mm in diameter and have 9–11 major septa. Septa are thin, straight, alternately long and short, and fibronormal in terms of microstructure. Major septa reach the center of the corallite. Corallite walls are almost indistinguishable from septa and dissepiments. In most corallites, the major septa are 2.0–3.5 mm long and minor septa are 0.8–2.4 mm long. Minor septa typically extend about 2/3 length of major septa to tabularium wall. Dissepimentarium is formed by 3–5 rows and is 0.3–2.7 mm. Tabularium has a diameter of on average 2.3 mm.

Longitudinal section description: Dissepiments are well developed in the peripheral part, elongate in form and not much inclined. Dissepimentarium rather wide, occupying about 2/3 of the diameter of the corallites and consisting of 3–5 rows of dissepiments which are an average of 2 mm long. Axial tabellae and periaxial tabellae are similarly inclined. Diameter of the tabularium varies around the average of 2.2 mm, from 1.8 to 3.0 mm. In the tabularium, the tabulae adjacent to the dissepimentarium have a slope of 25°–40°.

Remarks.—One of the so-called 'Devonian type corals' from Cheonseongri described by Yabe and Sugiyama (1940) was reidentified by Kato (1972) as *Arachnastraea kaipingensis* (Grabau). It was the first record of occurrence of *Arachnastraea* in Korea. *Arachnastraea manchurica* differs from *Arachnastraea kaipingensis* in corallite walls, columella and

Figure 3. 1, 2. *Arachnastraea manchurica* Yabe and Hayasaka; 1, transverse section ($\times 7$, KNUE 96201), 2, Longitudinal section ($\times 7.5$, KNUE 96215). 3–5. *Diphyphyllum delicatum* Minato and Kato; 3, transverse section showing both the early and mature stages ($\times 8$, KNUE 96219), 4, slightly obliquely cut longitudinal section ($\times 7$, KNUE 96229), 5, slightly obliquely cut transverse section ($\times 7$, KNUE 96217). 6. association of *Arachnastraea manchurica* and *Fusulinella* sp. ($\times 10$, KNUE 96199).

dissepimentarium. In the latter the corallum is cerioid-astraeoid and corallite walls are well developed, sharply zigzag and partially depressed. The dissepimentarium of the latter consists of 3-4 rows of regular dissepiments.

Family Lithostrotionidae d'Orbigny, 1851
Subfamily Diphyphyllinae Dybowski, 1873
Genus *Diphyphyllum* Lonsdale, 1845

Diphyphyllum Lonsdale, Hill, 1956, p. 283; Hill, 1981, p. 383.

Type species.—*Diphyphyllum concinnum* Lonsdale, 1845.

Diagnosis.—Fasciculate corallum, typically without columella. Septa short, continuous in dissepimentarium and amplexoid in tabularium. Columella absent or impersistent. Tabulae convex or flat, with downturned edges. Dissepimentarium narrow, composed of one or more rows of small dissepiments (slightly modified after Hill, 1956).

Remarks.—The species of *Diphyphyllum* may have a wide range of variability in terms of the structure, shape and mode of the tabulae. This genus has inner tabulae which are strongly arched, and each arch rests upon the arch below. In addition, Sando and Bamber (1985) mentioned that this genus is very similar to *Siphonodendron*, from which it differs by having flat or convex tabulae and by lacking a columella or having a thin, vertically discontinuous one.

Armstrong (1970) regarded a smaller group of species, such as *Diphyphyllum venosum*, *Diphyphyllum nesorakensis* and *Diphyphyllum klawockensis*, as having complete tabulae with broad flat tops and downturned edges that extend to the dissepimentarium without touching the lower tabulae.

The majority of the described species of *Diphyphyllum* indicated a late Early Carboniferous age (Minato and Kato, 1975). This genus is common in North America and is found exclusively in the shallow-water carbonate lithofacies (Sando and Bamber, 1985).

Diphyphyllum delicatum Minato and Kato, 1957

Figures 3-3—3-5

Diphyphyllum delicatum Minato and Kato, 1957, p. 137, text-figs. A-C; Minato and Kato, 1974, p. 56-60.

Material.—KNUE 96217-96245 (KNUEDY Locality 2). Only two specimens for this study were collected by the present authors from the measured stratigraphic section (see Figure 2).

Description.—*Transverse section description:* Corallum is compound, fasciculate and dendritic rather than phaceloid. Corallites are circular to subcircular. Corallites are closely adjacent, and are often in contact. Mature corallites range from about 6.7 to 11.4 mm in diameter and possess 18 to 25 major septa. Both major and minor septa are thin, fibronormal in terms of microstructure. Major septa are 1.5-2.2 mm in length, protruding 0.2-0.9 mm in tabularium, except for some major septa which are 0.9-1.1 mm in length. Minor septa are usually confined to adaxial first row of dissepiments, rarely protruding into second row of dissepiments, and are 0.25 to 0.38 mm in length. Dissepimentarium

ranges from 1.1 to 2.2 mm in width and consists of one to three rows of regular dissepiments. Tabularium varies from 4.1 to 6.4 mm in width and is open without any axial structure.

Longitudinal section description: Corallites are cylindrical and rather closely disposed. Dissepimentarium is 0.5 to 1.9 mm wide and consists of one to three rows of inclined, inflated to globose dissepiments. Tabulae are mostly complete, slightly concave in central part of the corallite, 4 to 9 in a vertical distance of 5 mm. However, they turn downward at an average angle of 32° before joining the dissepiments.

Remarks.—Our specimens differ slightly from Minato and Kato's (1975, pl. 9, figs. 2-6, pl. 10, figs. 1-4) species *Diphyphyllum delicatum*, which was described from the Upper Carboniferous Nagaiwa Series of northeast Japan, by having more numerous major septa, a wider dissepimentarium, and a more strongly developed row of dissepiments. Igo and Kobayashi (1980) described a new subspecies, *Diphyphyllum delicatum nishitamensis*, from the Itsukaichi District, Tokyo, Japan, which is similar to, but not conspecific with *Diphyphyllum delicatum* illustrated by Minato and Kato (1975). Igo and Kobayashi (1980) noted that *Diphyphyllum delicatum* and *Diphyphyllum delicatum nishitamensis* differ noticeably in the length of major and minor septa. The former is characterized by short major and minor septa, while the subspecies has longer septa compared with the size of the corallite.

As Minato and Kato (1957) mentioned, *Diphyphyllum* has a long stratigraphic range from the Lower Carboniferous to Permian, but this particular species is confined to the upper part of the Upper Carboniferous Geumcheon Formation in the Danyang area.

Discussion

One of the purposes of this study is to reexamine the Devonian corals mentioned by Yabe and Suzuki (1955). According to Kato (1972), Suzuki earlier collected several coral specimens in Gosuri, Danyang in 1944, but these materials are lost. Yabe and Suzuki (1955) reported the occurrence of the Devonian corals *Disphyllum* sp. and *Phillipsastraea* sp. Their figures 1 and 2 are index maps of the fossil locality, while figures 3 and 4 show the corals on the weathered surface of the limestone near Gosu Pass in Danyang area. The figures are not clear, but colony type and internal structure of corals were, however, distinguished.

On the basis of their figure 3, several clues to identification of the corals were found by the present authors. First of all, the corallites in figure 3 are compound, fasciculate and dendritic rather than phaceloid. Although Yabe and Suzuki (1955) identified them as *Disphyllum* sp., the branches of their coral specimens are too irregular to be those of *Disphyllum*. The second is that the septa are very short and the dissepimentarium are very narrow with one or two rows of small dissepiments. In longitudinal view, the tabulae are convex with downturned edges without columella. These are typical characters of *Diphyphyllum*. It is considered that the coral specimens described by Yabe and Suzuki (1955) are not of the Devonian genus *Disphyllum*, but the Carboniferous *Diphyphyllum*. *Disphyllum* sp. is illustrated only in figure 3 of

Yabe and Suzuki (1955), but they did not provide any illustrations of *Phillipsastraea* sp.

Furthermore, fusulinids and conodonts occur abundantly from the Geumcheon Formation. A number of fusulinids are observed together with corals in the same thin sections (Figure 3-6). Because the Carboniferous corals have long ranges, both fusulinids and conodonts may provide a useful criteria for understanding the paleoecology and determining the geologic age of the Geumcheon Formation.

Conclusion

Two species of rugose corals from the Geumcheon Formation in the Danyang area, Korea are described as *Arachnastraea manchurica* and *Diphyphyllum delicatum*. The corals indicate that the age of the Geumcheon Formation is middle Moscovian, Late Carboniferous.

Coral specimens from the Danyang area once illustrated as the Devonian corals *Disphyllum* sp. and *Phillipsastraea* sp. (Yabe and Suzuki, 1955), are considered Carboniferous corals, *Diphyphyllum* sp. and *Arachnastraea* sp. respectively.

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Cheonseongri 天聖里, Danyang 丹陽, Donggo Formation 東古層, Dosagok Formation 道士谷層, Gangneung 江陵, Geumcheon Formation 黔川層, Gosu 古藪, Hambaegsan Formation 咸白山層, Jangseong Formation 長省層, Jeongseon 旌善, Kohan Formation 古汗層, Manhang Formation 晩項層, Pyeongan Supergroup 平安累層群, Sindanyang 新丹陽, Taebaeg 太白, Yeongweol 寧越

Relation of growth rings to reproductive cycle in *Cryptopecten vesiculosus*, a dimorphic pectinid bivalve

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Abstract. The relation between growth rings and reproductive cycle in a dimorphic pectinid bivalve, *Cryptopecten vesiculosus* (Dunker, 1877) was examined histologically on the basis of semi-regularly collected samples from Sagami Bay. This pectinid is hermaphroditic. Male and female gonads ripen between June and September, and spawning occurs during July to November. A strong growth ring is formed just before spawning, and the first ring indicates that the specimens has reached the stage of sexual maturity. This means that growth rings are formed once a year after the individual reaches sexual maturity. No visual difference was detected in the gonad development between the two phenotypes; their gonadal weight indices are statistically identical throughout the year. Therefore the previous interpretation that the dimorphism represents discontinuous intrapopulational variation is upheld. The results of this study are applicable to life history analysis in extant and fossil populations.

Key words : Dimorphism, growth rings, life history, pectinid bivalve, reproductive cycle

Introduction

The pectinid bivalve, *Cryptopecten vesiculosus* (Dunker, 1877) is characterized by a few prominent commarginal growth rings, which consist of periodic changes in the convexity of the disc surface. It has been judged that the growth rings are caused by a growth pause during the reproductive season. Furthermore, *C. vesiculosus* has been considered a dimorphic species, because two discrete phenotypes exist in every population. One phenotype has highly elevated and generally quadrate radial ribs, while the other has low and generally rounded radial ribs. They have been called “Phenotype Q” and “Phenotype R”, respectively. These two phenotypes are strictly sympatric, and their allozyme patterns show no statistical difference. Consequently it has been believed that the dimorphism is due to discontinuous intrapopulational variation (Hayami, 1984 ; Sarashina, 1995).

Histological observations on the development of gonads through the year is vital to prove the assumptions mentioned above, as well as to trace a clear relation between growth rings and the reproductive cycle. The relation, if clarified, would become fundamental to analyses of life history (especially, age, lifespan, growth rate and mortality rate) not only in extant but also in fossil populations.

Material and method

Cryptopecten vesiculosus (Dunker, 1877) is distributed from the central part of Japan to the East and South China Sea. It is a lower sublittoral species, living commonly on sandy bottoms at the depth of 50–200 m (Hayami, 1984). Fossils of this species are also found abundantly in Early Pliocene and later marine deposits of Japan. Living individuals of *C. vesiculosus* were collected monthly to bimonthly between March 1997 and February 1998 almost at one and the same station, about 2 km west of the western end of Jōgashima Islet in the eastern part of Sagami Bay [35°08'N, 139°35'E, 80–85 m]. Table 1 shows the dates of dredging and the number of collected living individuals. The integrated relative frequency of the two phenotypes is almost identical with the ratio indicated by Hayami (1984) in samples Jg (1–26) collected during 1974–1983 at nearby stations in Sagami Bay, and statistically there is no significant difference.

To clarify the reproductive cycle and the shell size at sexual maturity, I observed the process of gametogenesis and determined the gonad developmental phase for many individuals in each phenotype. Collected specimens were anesthetized with 0.01% 2-phenoxyethanol methylene glycol diluted with sea water, and then fixed for 48 hours in a solution of 10% formaldehyde. The dissected gonadal tissue of each specimen was excised and weighed after rinsing in water. It was dehydrated through a graded series of ethanol and benzol, and then embedded in paraffin (melting

Table 1. Collecting dates and the number of individuals of *Cryptopecten vesiculosus*.

| Date | N _O | N _R | N | P | σ_P |
|---------------|----------------|----------------|-----|------|------------|
| Mar. 25, 1997 | 9 | 14 | 23 | 0.61 | 0.10 |
| May 1, 1997 | 42 | 30 | 72 | 0.42 | 0.06 |
| Jun 4, 1997 | 26 | 25 | 51 | 0.49 | 0.07 |
| Jul. 29, 1997 | 54 | 30 | 84 | 0.36 | 0.05 |
| Sep. 30, 1997 | 79 | 67 | 146 | 0.46 | 0.04 |
| Nov. 19, 1997 | 35 | 28 | 63 | 0.44 | 0.06 |
| Dec. 18, 1997 | 44 | 31 | 75 | 0.41 | 0.06 |
| Feb. 16, 1998 | 36 | 36 | 72 | 0.50 | 0.06 |
| Total | 325 | 261 | 586 | 0.45 | 0.02 |

N: Total number of individuals; N_O: Number of individuals belonging to Phenotype Q; N_R: Number of individuals belonging to Phenotype R; $P = N_R/N$; σ_P : Standard error.

point: 56–58°C). Thin transverse sections of the gonadal tissue were prepared at intervals of 8 μm and stained with Lillie–Mayer's hematoxylin–eosin. The stained thin sections were observed and photographed using an Olympus model BX50 optical microscope. Based on histological examination of the thin-sectioned gonadal tissue, each specimen was assigned to a specific gonad developmental phase: early active phase (EA), late active phase (LA), ripe phase (R), partially spawned phase (PS), or spent phase (S). Further, the mean gonad index [(gonad weight \times 100)/soft body weight] was calculated for sexually mature individuals to analyze the annual reproductive cycle of the population.

The results were analysed to determine whether or not growth rings can be used as an index of age. Shell height from the umbo to each growth ring, normal to the hinge line, was measured in all the samples with a digimatic caliper (accuracy ± 0.02 mm). In addition, the numbers of growth rings was counted, and the mean shell height at each growth ring was calculated for individuals with more than three growth rings. The fit of these mean values to von Bertalanffy, Gompertz and logistic curves was examined. These curves are expressed by the following formulae:

$$H(B) = K(1 - \exp(-a - Rt)) \quad (\text{von Bertalanffy curve})$$

$$H(G) = K \exp(-a \exp(Rt)) \quad (\text{Gompertz curve})$$

$$H(I) = K / (1 + \exp(a - Rt)) \quad (\text{logistic curve})$$

where H is the size of the animal (shell height in this case) at age t , K is the upper limit of the curve, R is the specific growth rate, and a is a constant defined by the initial size ($= H_0$) at $t = 0$.

Results

1. The reproductive cycle of *Cryptopecten vesiculosus*

Spermatozoa were observed in the milky white proximal part of the crescentic gonad and oocytes in the orange distal part. In consequence, it was confirmed that *Cryptopecten vesiculosus* is hermaphroditic and that the shell dimorphism is never sexual. Histological examination of gonadal tissue revealed that gametogenesis in *C. vesiculosus* is essentially similar to that in the commercial scallop *Azumapecten farreri nipponensis*, which was analyzed by Kanno and Tanita (1961), though that species is dioecious. Following the general classification of gametogenetic phases in bivalves proposed by Ropes (1968) and Sato (1995), the reproductive cycle of *C. vesiculosus* is described below.

Early active phase (Figure 1A, B)

In the male gonad of this phase, many spermatogoniums about 8 μm in diameter, each of which consists of a nucleus and thin nucleoplasm, appear along the inner periphery of the alveolar walls. Further, spermatocytes about 5 μm in diameter proliferate towards the lumina from the alveolar walls. Oogoniums and oocytes which protrude inside the alveolar walls are seen in the female gonad. The oogoniums range from 15 to 20 μm and the oocytes range from 20 to 30 μm in diameter. Each oocyte has a nucleus about 15–20 μm , which contains a nucleolus approximately 4 μm in diameter.

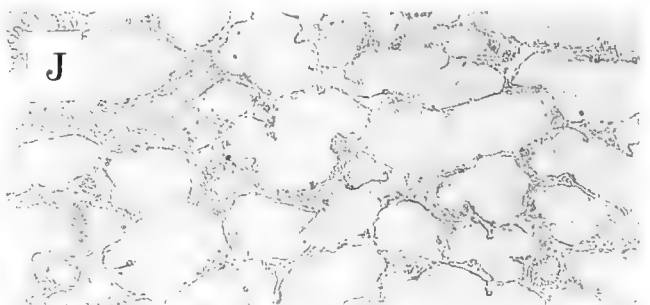
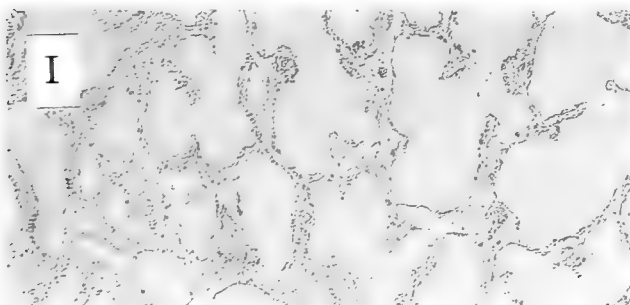
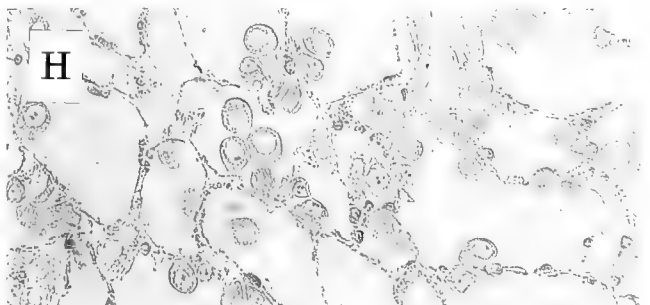
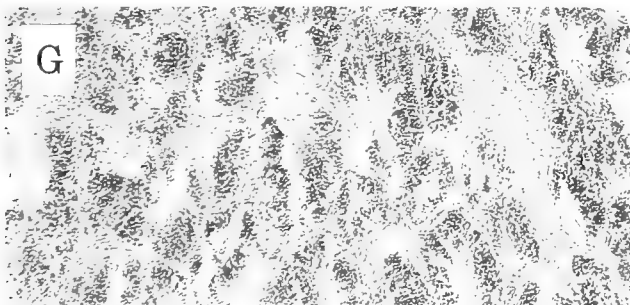
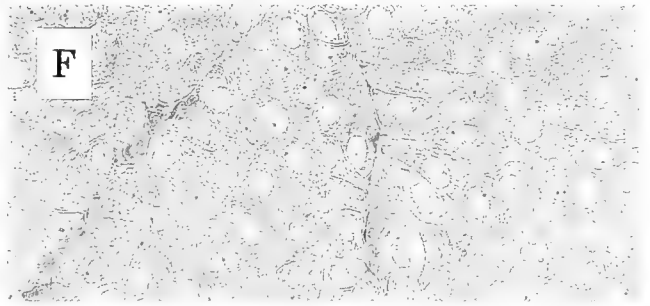
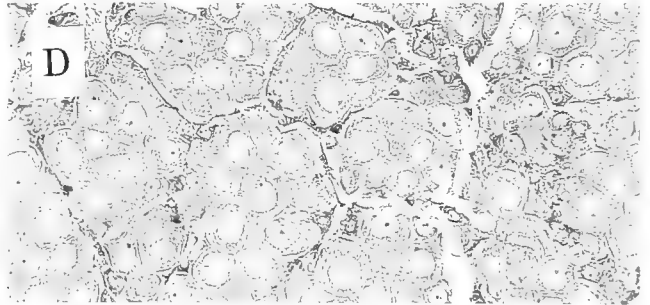
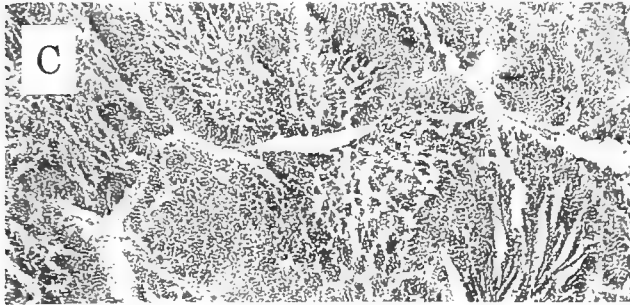
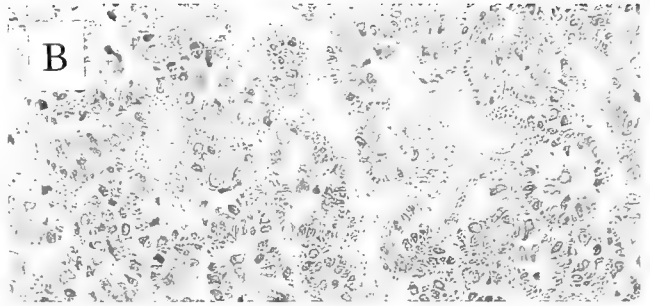
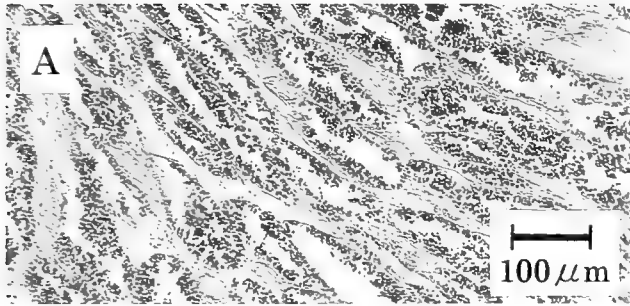
Late active phase (Figure 1C, D)

Many spermatocytes are seen in the male gonad of this phase. Spermatids about 4.5 μm in diameter also are seen, and they form dense masses near the center of the alveoli. A transformation of the spermatids results in the appearance of sperm. They form weak columns toward the center of the alveoli. Oocytes in the late active phase are mostly rounded and larger than in the early active phase. Some oocytes are attached to the basement membrane of the alveoli, but most are free in the lumina. In this phase oogoniums and ripe oocytes coexist within one and the same female gonad.

Ripe phase (Figure 1E, F)

In this phase, spermatozoa or free oocytes occupy the major space in the gonadal tissue. The head of each sperm is corn-shaped and about 2 μm in length. Oocytes are free in the lumina of the alveoli. Each oocyte about 60 μm in diameter contains a round or oval nucleus ranging from 30 to 35 μm , and each nucleus possesses one small opaque basophilic nucleolus about 5 μm in diameter. Ripe gonads typically have a dense appearance because the alveoli are crowded together and are filled with large oocytes or numer-

Figure 1. Optical photomicrographs of sections of male and female gonadal tissues in *Cryptopecten vesiculosus* in each phase of the reproductive cycle. The scale bar in A pertains as well to B–J. All specimens were collected from Sagami Bay. **A**: Early active phase of a male collected on 16 February 1998. **B**: Early active phase of a female collected on 16 February 1998. **C**: Late active phase of a male collected on 25 March 1997. **D**: Late active phase of a female collected on 25 March 1997. **E**: Ripe phase of a male collected on 29 July 1997. **F**: Ripe phase of a female collected on 29 July 1997. **G**: Partially spawned phase of a male collected on 19 November 1997. **H**: Partially spawned phase of a female collected on 19 November 1997. **I**: Spent phase of a male collected on 18 December 1997. **J**: Spent phase of a female collected on 18 December 1997.



ous spermatozoa.

Partially spawned phase (Figure 1G, H)

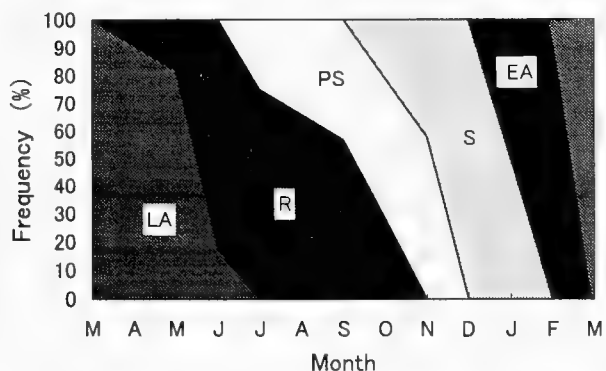
In the male gonad of this phase, spermatozoa are still present near the center of alveoli, but they are substantially less numerous than in the ripe phase. A few large ripe oocytes remain free in the lumina of some alveoli of the female gonad.

Spent phase (Figure 1I, J)

In this phase the alveoli of male and female gonads contain few or no spermatozoa or oocytes. Their lumina characteristically are open.

Seasonal change in the relative frequency of the five gametogenetic phases in the samples of *Cryptopecten vesiculosus* from Sagami Bay in 1997–1998 is shown in Figure 2. Individuals belonging to the late active phase amount to than 80% of the population between March and May, while ripe-phase individuals become dominant between June and September. Some individuals begin to spawn in July, and almost all individuals reach the spent phase in December. After that, the proportion of individuals in the early active phase increases gradually. The mean

Phenotype Q



Phenotype R

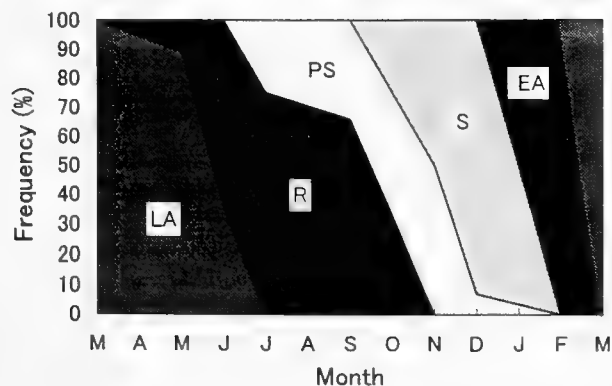


Figure 2. Diagram showing the change of relative frequency (%) of gonad development stages through a year (1997–1998) in the two phenotypes of *C. vesiculosus*. EA: Early active phase, LA: Late active phase, R: Ripe phase, PS: Partially spawned phase, S: Spent phase.

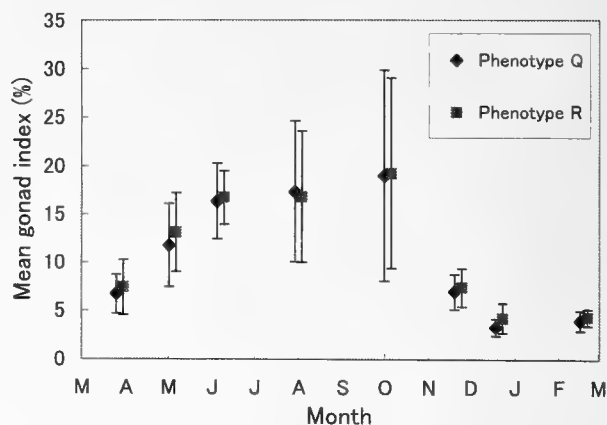


Figure 3. Seasonal changes in mean gonad index [(gonad weight \times 100)/soft body weight]. The mean and the range of one standard deviation (vertical bar) are indicated. No statistical difference was detected between the two phenotypes.

gonad index increases from March to June, scarcely changes from June to September, and decreases significantly after September (Figure 3). Therefore, the reproductive season of *C. vesiculosus* is considered to be a relatively long period between early June and late September. Neither visual nor statistical difference was detected between the two phenotypes in their reproductive cycles and seasonal changes of gonad indices.

2. The size at sexual maturity

Table 2 indicates the frequencies of juvenile, semimature and mature specimens and their relation to shell height in the samples collected during the reproductive season. Reproductive cells were not observed at all in individuals smaller than 10 mm in shell height, and gonadal tissue, if present, was so small that they are regarded as juvenile. Individuals larger than 14 mm in shell height can be regarded as mature. Most individuals between 10 and 14 mm possess only a few reproductive cells. They are regarded here as semimature, and spawn like mature individuals. It is, therefore, considered that individuals of *C. vesiculosus* reach sexual maturity at about 10 mm in shell height.

3. Formation of growth rings

The position of growth rings was observed, and the following four states are discriminated by the relation between the last growth ring and the ventral margin (Figure 4).

State A (Figure 4-1a, 1b)

Individuals with swelling of the marginal area

State B (Figure 4-2a, 2b)

Individuals with a growth ring just on the ventral margin

State C (Figure 4-3a, 3b)

Individuals with slight new shell growth (<5 mm) after the formation of last ring

State D (Figure 4-4a, 4b)

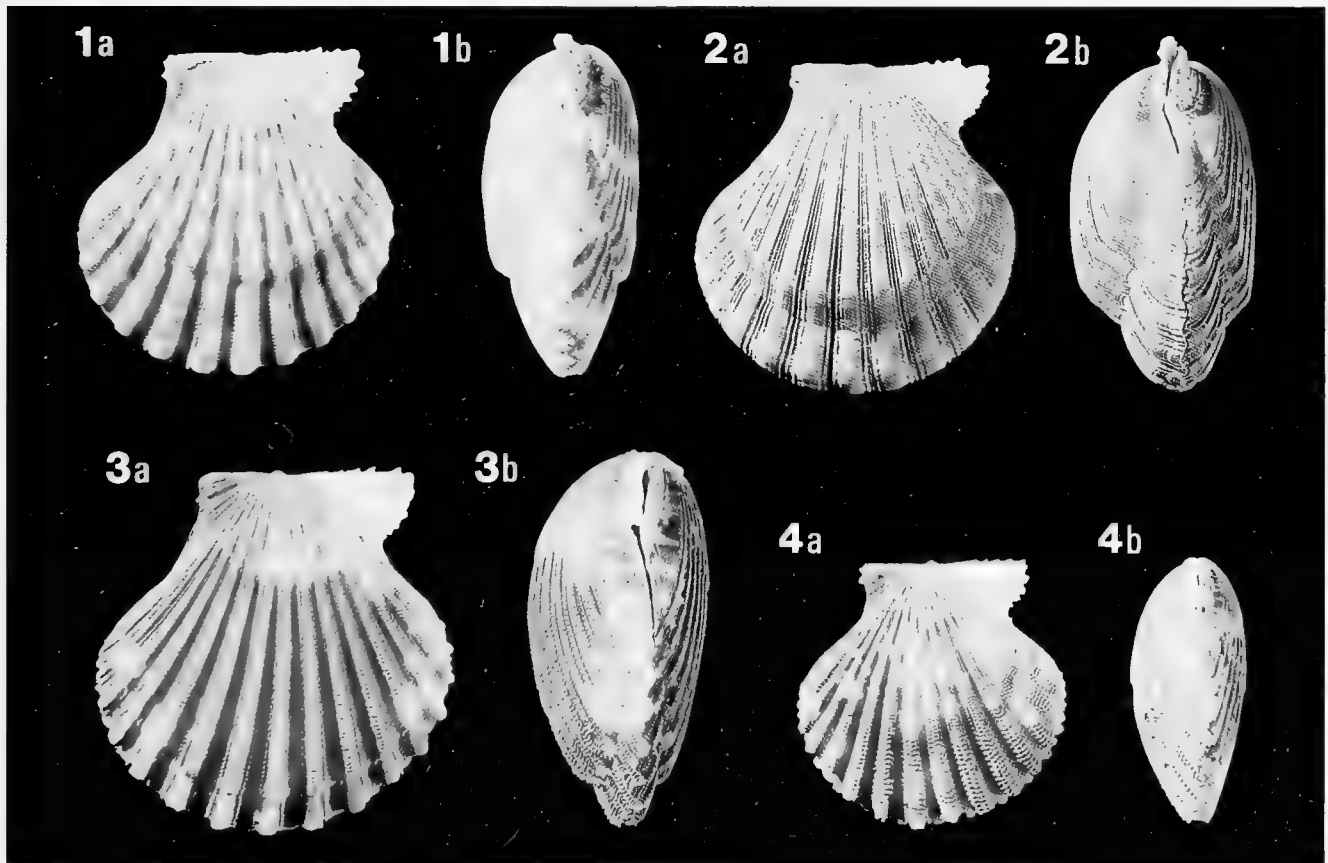
Individuals without swelling of the marginal area

The seasonal change in the relative frequency of these states is shown in Figure 5. In spring, many individuals in

Table 2. Distribution of the stages of sexual maturation in relation to shell height in the samples of *Cryptopecten vesiculosus* collected from Sagami Bay during the reproductive season.

| Shell height (mm) | Sampling date | | | | | | | | | | | | | | |
|----------------------|---------------|---|----|--------|---|----|---------|----|---|----------|---|----|---------|---|----|
| | May 1 | | | June 4 | | | July 29 | | | Sept. 30 | | | Nov. 19 | | |
| | A | B | C | A | B | C | A | B | C | A | B | C | A | B | C |
| 6- 8 | | | | | | | 1 | | | | | | | | |
| 8-10 | 1 | | | | | | 1 | | | | | | 1 | | |
| 10-12 | | | | 1 | | | 1 | 9 | | | 4 | 1 | | 6 | 1 |
| 12-14 | | 1 | | | 2 | | | 12 | 3 | | 3 | 4 | | 2 | 3 |
| 14-16 | | | | | | 1 | | | 8 | | 1 | 7 | | 2 | 9 |
| 16-18 | | | 6 | | | 3 | | | 4 | | | 14 | | | 4 |
| 18-20 | | | 9 | | | 16 | | | 5 | | | 28 | | | 4 |
| 20-22 | | | 11 | | | 9 | | | 6 | | | 25 | | | 12 |
| 22-24 | | | 2 | | | 6 | | | 3 | | | 15 | | | 7 |
| 24-26 | | | 1 | | | 1 | | | 1 | | | 4 | | | |
| 26-28 | | | | | | | | | 1 | | | | | | |

A: Juveniles, B: Semimature individuals, C: Mature individuals

**Figure 4.** Extant sample of *Cryptopecten vesiculosus* collected from Sagami Bay. **1:** Individual of Phenotype Q with swelling of marginal area (State A) collected on 1 May 1997, (a) right view, (b) anterior view; **2:** Individual of Phenotype R with a growth ring just on ventral margin (State B) collected on 30 September 1997, (a) right view, (b) anterior view; **3:** Individual of Phenotype Q with slight new growth (<5 mm) after the formation of the last growth ring (State C) collected on 16 February 1997, (a) right view, (b) anterior view; **4:** Individual of Phenotype Q without swelling of marginal area (State D) collected on 25 March 1997, (a) right view, (b) anterior view. All figures magnified about 1.9 times.

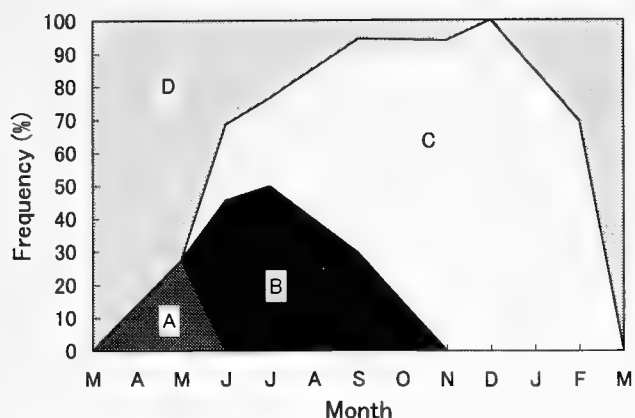


Figure 5. Diagram showing the relative frequency (%) of four states of shell growth. State A: Individuals with a swelling of the marginal area, State B: Individuals with a growth ring just on the ventral margin, State C: Individuals with slight new growth (<5 mm) after the formation of the last growth ring, State D: Individuals without swelling of the marginal area.

state A appear simultaneously with the early development of the gonads. Individuals in state B become most abundant in July. This produces a temporary cessation of shell growth. On the other hand, the proportion of individuals in state C gradually increases from June and becomes almost 100% in November. The result indicates that the growth rings are formed once a year and can be used as an index of age.

The shell height at each growth ring was measured in all individuals (Figure 6). The first growth ring is formed at a height of 9–11 mm in most individuals. Using individuals with more than three growth rings, I calculated the mean shell height at each growth ring. I then examined how the data adapt to the von Bertalanffy, Gompertz and logistic growth curves. The results of computation show that the shell growth of this species fits well to all of the three curves, especially to the Gompertz curve (Table 3).

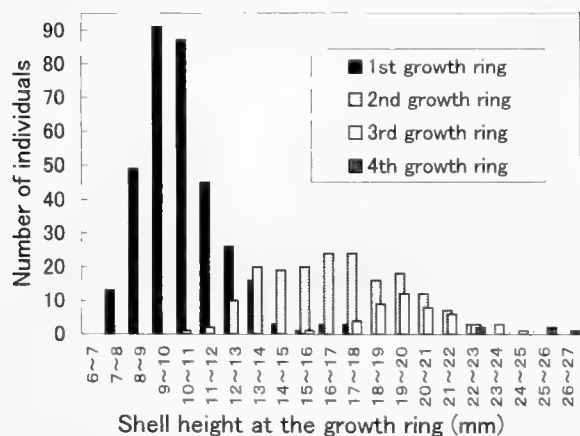


Figure 6. Frequency distribution of shell height at each growth ring in the samples of *Cryptopecten vesiculosus* collected during March 1997–February 1998.

Table 3. Mean shell height at each growth ring and its adaptability to three theoretical growth curves of the extant sample of *Cryptopecten vesiculosus* collected from Sagami Bay.

| Age (years) | 1 | 2 | 3 | 4 |
|--------------------------|---|-------|-------|-------|
| Mean shell height (mm) | 10.20 | 17.45 | 21.91 | 24.33 |
| Standard deviation | 1.472 | 2.295 | 1.824 | 1.634 |
| Number of individuals | 337 | 176 | 47 | 5 |
| Calculated values (mm) | | | | |
| von Bertalanffy curve | 10.20 | 17.50 | 21.80 | 24.35 |
| Gompertz curve | 10.20 | 17.43 | 21.98 | 24.30 |
| logistic curve | 10.20 | 17.41 | 22.16 | 24.16 |
| Calculated formula curve | | | | |
| von Bertalanffy curve | $H(B) = 28.02 (1 - \exp(-0.453 - 0.527t))$ | | | |
| | $r = 0.999$ | | | |
| Gompertz curve | $H(G) = 26.24 \exp(-2.180 \exp 0.837t)$ | | | |
| | $r = 1.000$ | | | |
| logistic curve | $H(I) = 25.16 / (1 + \exp(1.574 - 1.192t))$ | | | |
| | $r = 0.998$ | | | |

Discussion

The spawning season of *Cryptopecten vesiculosus* begins in early June and extends to late September, continuing for a comparatively long period. No visual difference was detected in the gonad development between the two phenotypes; seasonal changes of weight indices of the gonads show very similar patterns (Figure 3). Therefore, the previous interpretation that the dimorphism is due to discontinuous intrapopulation variation is upheld.

Growth rings are formed clearly on the shell surface in many bivalves and are often useful in determining the age of individuals and their growth rate. Kennish (1980) called the strong internal growth lines of bivalves growth breaks. The growth breaks reflect various environmental or physiological stresses such as freeze shocks (in winter), heat shocks (in summer), thermal shocks, shell-margin abrasions, spawning, neap tides, and storms. There is often a direct relationship between internal growth breaks and external growth rings (Dillon and Clark, 1980). Therefore, growth rings are considered to be formed by the same factors as internal growth breaks. Among various bivalves, growth rings are produced by freeze-shock breaks (e.g., *Pecten maximus*, Mason, 1957; *Tivela stultorum*, Hall et al., 1974; *Modiolus modiolus*, Seed and Brown, 1978; *Aequipecten opercularis*, Broom and Mason, 1978; *Mya arenaria*, Goshima, 1982; *Phacosoma japonicum*, Tanabe, 1988) or heat-shock breaks (e.g., *Mercenaria campechiensis*, Jones et al., 1990; *Chamelea gallina*, Ramón and Richardson, 1992). Spawning breaks are also used to assess annual growth increment in some species (e.g., *Spisula solidissima*, Jones et al., 1978; *Arctica islandica*, Thompson et al., 1980).

Generally, a growth ring is formed by an interruption of the shell growth. Because various states of the ventral margin are observed within each simultaneous sample of *C. vesiculosus*, it is unlikely that growth cessation due to thermal stress or any other such instantaneous events.

The cause of ring formation may be better understood, if gametogenesis and spawning are taken into consideration. Some individuals of *C. vesiculosus* begin to spawn in July, but the spawning season extends until the end of September (Figure 2). Moreover, the number of individuals with newly grown shell after the formation of the last growth ring gradually increases from June on (Figure 5). Consequently, it is obvious that a growth ring is formed just before spawning, when the gonad is still filled with sperm and free oocytes. On the other hand, the gonad index becomes much smaller in individuals with newly grown shell. Reproduction is one of the most energy-consuming physiological activities; it is therefore likely that gametogenesis exerts a great influence on shell formation.

In this connection Gutsell (1930) discussed the formation of growth rings in *Argopecten irradians*. He believed that a decline of metabolic activity, which is related to the development of eggs and sperm rather than spawning, must be responsible for the growth cessation. It is considered that the growth ring of *C. vesiculosus* is also formed by growth cessation in relation to energy consumed in gametogenesis. The surface swelling before the formation of a growth ring may be caused by the retardation of shell growth. The growth rings of *C. vesiculosus* must be produced just before spawning. The present interpretation is in agreement with the trade-off relationship between somatic and reproductive cells.

Since mature reproductive cells were observed in the individuals larger than 10 mm in shell height, sexual maturity may be attained at this size. The first growth ring is comparatively weak and is formed at 9–11 mm in shell height in most individuals (Figure 6). This is consistent with the sexual maturity size. Therefore, the growth rings of *C. vesiculosus* are considered to be formed once a year after the individual has reached sexual maturity. The growth rings are thus useful for determining the age of extant specimens and can presumably be applied to fossils as well. The shell growth pattern fits well with the von Bertalanffy, Gompertz and logistic curves. The shell height indicates a decrease in specific growth rate as the shell size approaches its upper limit of 26–28 mm. The number of growth rings indicates that the maximum lifespan of *C. vesiculosus* is four or five years.

The absolute growth pattern, however, may change geographically and chronologically within one and the same species. In fact, the growth rate and ultimate size in the samples from Sagami Bay are significantly smaller than those of some other extant and fossil samples, as shown by Hayami (1984, fig. 7). The exact age distribution and mortality rate are difficult to obtain from the present samples, because juvenile individuals smaller than 10 mm in height are not present in most samples and may have passed through the mesh of the dredging gear. It is also not clear whether the first ring is formed during the first year. However, the relation between growth rings and the reproductive cycle has been made very clearer through the present study.

Such prominent growth rings occur in some other pectinids; e.g. *Swiftopecten swiftii*, *Chlamys cosibensis* (a fossil species), and *Decatopecten striatus*. Although more

detailed study is necessary for each species, the mode and periodicity of growth rings are very similar in these species to those of *C. vesiculosus*. It is likely that gametogenesis is related to the formation of growth rings in those species also. It is expected that applying the knowledge about growth rings will clarify the life history of fossil populations and their evolution.

On the other hand, in many other pectinids periodical growth breaks, if present, are scarcely accompanied by surface swelling. Even in *C. vesiculosus*, Pleistocene fossil populations generally show weaker surface convexity between growth rings than the extant populations. The most plausible explanation in my mind is that the degree of trade-off between the gametogenesis and body growth actually varies among the pectinids species. In other words, the prominent growth rings in the extant populations of *C. vesiculosus* may be the product of more exhaustive trade-off than in many other pectinids and in the fossil populations of this species.

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行事予定

- ◎第148回例会は、1999年6月26日(土)～6月27日(日)に、「兵庫県立人と自然の博物館」で開催されます。一般講演の申し込み締切は5月7日です。6月26日にシンポジウム「日本の陸生哺乳類の起源、世話人：小澤智生・河村善也」が行われる予定です。会期中の宿の確保が難しい可能性があります。早めに宿を確保されることを希望される方は学会ホームページ (<http://ammo.kueps.kyoto-u.ac.jp/palaeont>) の年次大会のページに宿の一覧が掲載されています。
- ◎2000年年会・総会は、2000年1月28日(金)～1月30日(日)に「早稲田大学」で開催されます。一般講演の申し込み締め切りは1999年12月3日、シンポジウムの企画申し込み締切は1999年3月末日です。
- ◎第149回例会(開催予定時期：2000年の6月末頃)には、「群馬県立自然史博物館」から開催申し込みがありました。
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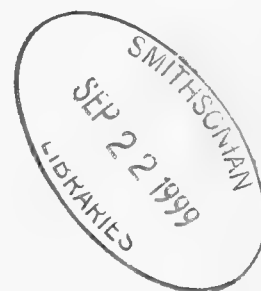
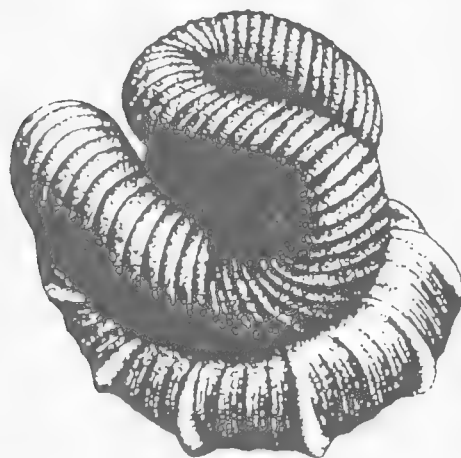
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Cover : Idealized sketch of *Nipponites mirabilis* Yabe, a Late Cretaceous (Turonian) nostoceratid ammonite. Various reconstructions of the mode of life of this species have been proposed, because of its curiously meandering shell form (after T. Okamoto, 1988).

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Three Ordovician cephalopods from the Jigunsan Formation of Korea

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Abstract. Cephalopod species previously described from the Middle Ordovician Jigunsan Formation of Duwibong type Joseon Supergroup of Baegunsan Syncline, Kangweondo in Korea were re-examined taxonomically based on the type and figured specimens and newly collected ones. Three species, *Holmiceras coreanicum* (Kobayashi, 1927), *Sactorthoceras makkolense* (Kobayashi, 1927), and *Kotoceras grabau* (Kobayashi, 1927) are described. Each species was restudied and compared with closely related species described by Kobayashi (1927, 1934); respective lectotypes are also designated herein. In this study, *Sigmorthoceras coreanicum*, based on its sigmoidally curved conch, was identified as belonging to *Holmiceras* which is characterized by the early loosely gyroceraconic shell portion. *Sinuitopsis kochirien-sis*, previously identified as an Ordovician gastropod, is a juvenile shell of *H. coreanicum*, judging by the number of the volutions and prominent shell surface. Three species belonging to *Sactorthoceras* and also *Cycloceras taihakuense* were regarded, based on the existence or nonexistence of the preserved shell and the imploded internal structure, as junior synonyms of *Sactorthoceras makkolense* in a broad sense. *Kotoceras frechi* was rejected as an invalid taxon, since its septal angulation, broader siphuncle and rapid expansion of the conch are characteristics caused by secondary deformation.

Key words : cephalopods, gyroceraconic, lectotype, Middle Ordovician, secondary deformation, synonym

Introduction

Paleontological study of the invertebrate fauna from the Cambro-Ordovician formations in Kangweondo, Korea was initiated by Kobayashi (1927). At that time, he identified three units (fossil beds 13, 14, and 15) as the "Chikunsan fossil beds". From these beds, he described 16 nautiloid species belonging to 8 genera from the Maggol, Hwarari and Hwang-jiri areas. He mentioned that the cephalopods from the "Jigunsan fossil beds" show an affinity with the Chazy of North America, while the trilobites and brachiopods show European affinity. Kobayashi (1934) subsequently described a great number of cephalopod fossils which belong to 58 species of 29 genera, revising 11 hitherto described species, and stated that the Jigunsan cephalopod fauna is diagnosed by the age of orthoceroid divergence in cephalopod macroevolutionary history. Later, Kobayashi (1966) made a comprehensive compilation of the Cambro-Ordovician formations and faunas of South Korea and divided the Middle Ordovician sequence of the Duwibong type Joseon Supergroup into five cephalopod assemblage zones i.e., *Manchuro-ceras*, *Polydesmia*, *Sigmorthoceras*, orthoceroid, and actinoceroid Zones in ascending order.

The Korean Ordovician cephalopods have been studied both taxonomically and biostratigraphically by Kobayashi (1927, 1934, 1966, 1969, 1977a, 1977b, 1978) and have not been revised by any subsequent researcher. The series of Kobayashi's works provides important phylogenetic clues and insight into the Asiatic and worldwide Ordovician paleogeography of fossil cephalopods. However, some Korean cephalopod specimens described by Kobayashi require additional restudy in view of the current knowledge of cephalopod taxonomy.

This paper aims to re-examine the systematics and taxonomy of three Ordovician cephalopod species from Korea on the basis of Kobayashi's (1927, 1934) type specimens and newly collected specimens from the type localities and other new localities.

Geological setting

The Cambro-Ordovician deposits are widely distributed in Kangweon-do, Korea. They have been divided into five types, based on the lithology and fauna; viz., Duwibong, Yeongweol, Jeongseon, Pyeongchang, and Mungyeong types (Kobayashi *et al.*, 1942). The cephalopod specimens

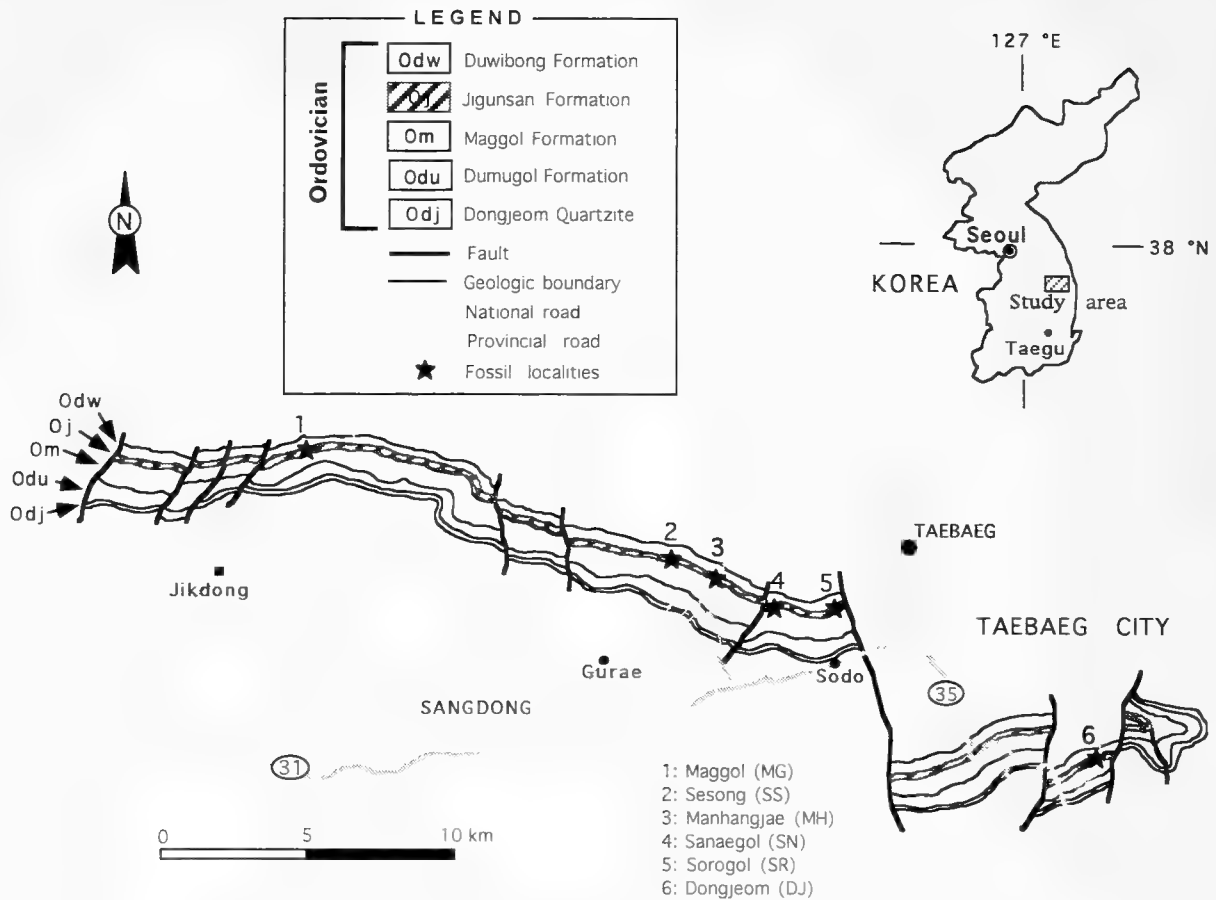


Figure 1. Geologic map of the study area, showing the cephalopod localities.

used in this study were collected from the Jigunsan Formation, Upper Joseon Supergroup which extends from east to west in the southern limb region of the Duwibong type Joseon Supergroup of the Baegunsan Syncline (Figure 1).

The Jigunsan Formation originally named as the "Chikunsan Shale" by Yamanari (1926), is about 50 m thick, conformably covers the Maggol Formation and grades into the overlying Duwibong Formation (Figure 2). This formation can be traced from east and west in the Taebaeg region. The Jigunsan Formation is lithostratigraphically divided into the lower, middle, and upper members. The lower member is essentially non-fossiliferous and consists mainly of black shale containing a little calcareous material; the middle member is composed of "worm-eaten" bioturbated limestone and vermicular shale intercalated by three or four limestone beds, each about 50 cm thick, and has yielded a large number of trilobites; the upper member consists of limestone and bioclastic grainstone with intercalating calcareous shale. The amount of carbonate gradually increases toward the top of the sequence and ultimately grades into the limestone of the Duwibong Formation; this member has yielded a rich cephalopod fauna.

The Jigunsan Formation is especially well exposed in the Sanaegol section (Figures 1, 2). It consists mainly of black

shales and thin beds of calcareous nodules, in which orthoconid and lituitid nautiloids occur. The lower member is almost barren of fossils; the middle member is characterized by the abundant occurrence of *Holmiceras*; the upper member is represented by bioclastic grainstone with intercalating calcareous shale and contains abundant ormoconid cephalopods.

According to Kobayashi (1934, 1966), the Jigunsan Formation is correlated with the Llandeilo in the European succession and the Chazy in the American sequence. Shimizu and Obata (1935b) described three graptolite species from the formation and correlated it with the Lower Llandeilian *Diplograptus teretiusculus* and *Nemagraptus gracilis* Zones in the Glenkiln Shale, England and Pingliang Shale of Gansu Province in North China. Shikama and Ozaki (1969) distinguished three assemblage zones in the Jigunsan Formation in the Dongjeom area, namely, the *Orthis nipponica*, *Basilicus deltacaudus*, and *Basilicus yokusensis* Zones in ascending order, based on the macrofossils collected by a member of the Yokohama Geologists Club in 1967 (Ozaki and Ogino, 1968).

The Jigunsan trilobite fauna has been studied in detail by Lee *et al.* (1980), who described 15 species belonging to 5 genera and correlated the formation with the Llandeilo to

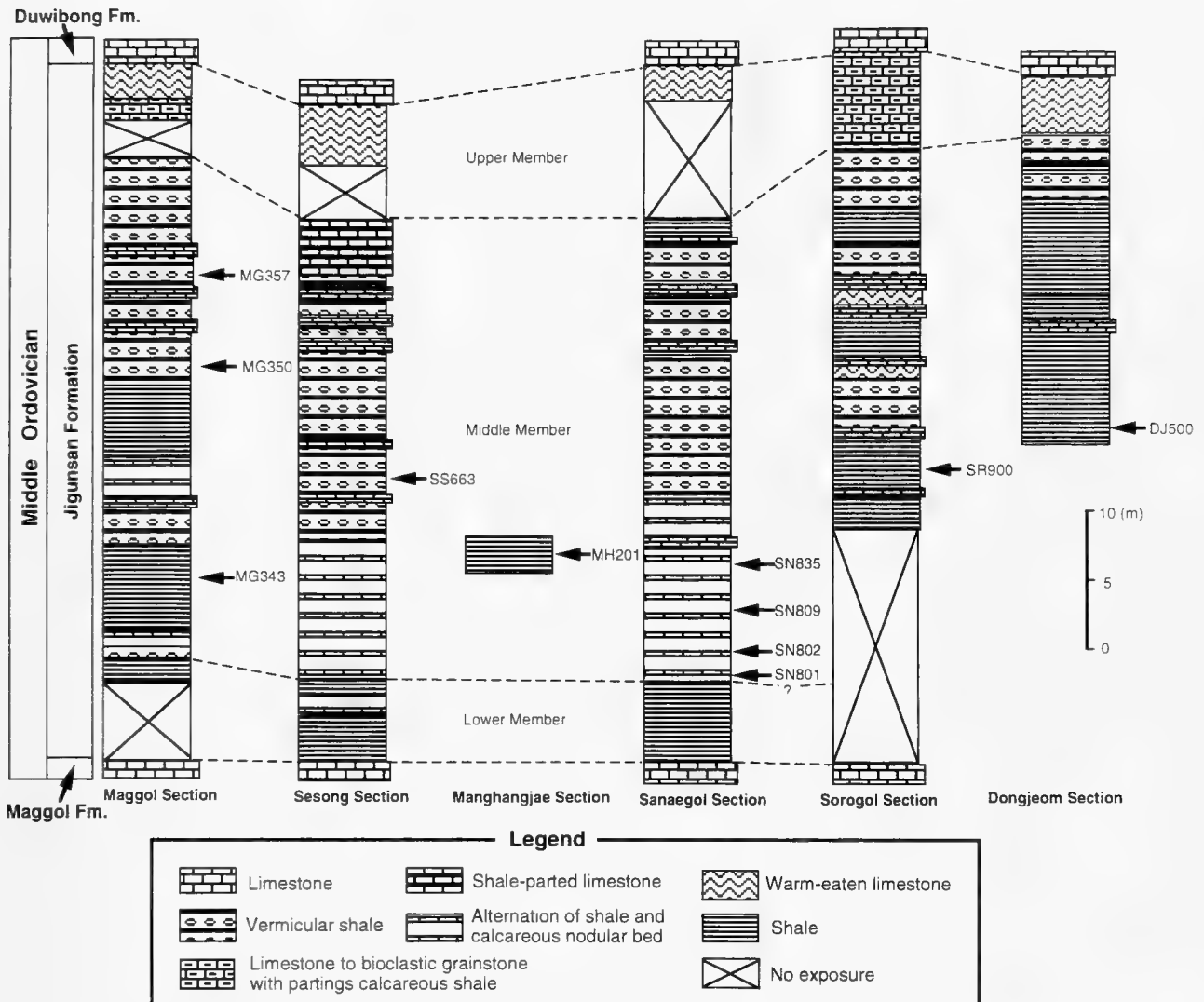


Figure 2. Geological columns of the Jigunsan Formation in the study area, showing the horizons of the cephalopod localities.

lower Caradoc interval in Europe.

Lee and Lee (1986) established a conodont biozone in the middle and upper parts of the Jigunsan Formation, namely, the *Eoplacognathus suecicus*-*Eoplacognathus jigunsanensis* Assemblage Zone. These authors correlated the conodont fauna with the *Eoplacognathus suecicus*-*Acontiodus?* *linxiensis* Zone of the lower Upper Majiagou Formation in North China and with the Lower to Middle Llanvirn in the European type section. They also suggested that the Jigunsan Formation was deposited in a deep shelf environment, based on the conodont fauna.

Materials

Most cephalopod specimens described by Kobayashi were collected from Maggol in Korea, where strata indicative

of the western part of the Duwibong type Joseon Supergroup are exposed (Loc. 1 in Figure 1). The list of type specimens re-examined in this study is shown in Table 1. The cephalopod type specimens in Table 1 are housed in the University Museum, University of Tokyo (UMUT).

Fifty-seven specimens listed in Table 2 were used for comparison with Kobayashi's type specimens. These new and unstudied specimens were collected by the present author and K. Tanabe on three occasions during May to August, 1997. All of them were discovered from the Middle Ordovician Jigunsan Formation in Kangweondo, Korea. They are deposited in the Department of Earth Science, Teacher's College, Kyungpook National University (KPE prefix), Taegu, Korea.

Table 1. List of cephalopod type specimens which were described by Kobayashi (1927, 1934) from the Jigunsan Formation and are re-examined in this study.

| Registered no. | Scientific name | Locality | Type |
|----------------|------------------------------------|----------|----------|
| UMUT PM 8 | <i>Sigmorthoceras coreanicum</i> | Maggol | Syntype |
| UMUT PM 9 | <i>Sigmorthoceras coreanicum</i> | Maggol | Syntype |
| UMUT PM 651 | <i>Sigmorthoceras coreanicum</i> | Maggol | Syntype |
| UMUT PM 6 | <i>Sactorthoceras makkolense</i> | Maggol | Syntype |
| UMUT PM 7 | <i>Sactorthoceras makkolense</i> | Maggol | Syntype |
| UMUT PM 660 | <i>Cycloceras</i> sp. | Hwangji | Syntype |
| UMUT PM 570 | <i>Sinuitopsis kochiriensis</i> | Hwangji | Syntype |
| UMUT PM 571 | <i>Sinuitopsis kochiriensis</i> | Hwangji | Syntype |
| UMUT PM 634 | <i>Kawasakiceras densistriatum</i> | Maggol | Holotype |
| UMUT PM 652 | <i>Sigmorthoceras sigmoidale</i> | Maggol | Holotype |
| UMUT PM 657 | <i>Cycloceras taihakuense</i> | Maggol | Paratype |
| UMUT PM 658 | <i>Cycloceras taihakuense</i> | Maggol | Paratype |
| UMUT PM 659 | <i>Cycloceras taihakuense</i> | Maggol | Paratype |
| UMUT PM 650 | <i>Sactorthoceras gonioseptum</i> | Maggol | Holotype |
| UMUT PM 643 | <i>Sactorthoceras shimamurai</i> | Maggol | Holotype |

Table 2. List of cephalopod specimens from the Middle Ordovician Jigunsan Formation, Kangweondo, Korea.

| Species | Locality | No. of specimens |
|----------------------------------|--|------------------|
| <i>Holmiceras coreanicum</i> | SN801, SN802, SN809, SN835, DJ500, MH201 | 32 |
| <i>Sactorthoceras makkolense</i> | SN802, SN809, SN835, DJ500 | 15 |
| <i>Kotoceras grabau</i> | SR900, SS663, MG343, MG350, MG357 | 10 |

Systematic paleontology

Subclass Nautiloidea
 Order Tarphycerida
 Family Lituitidae
 Genus ***Holmiceras*** Hyatt, 1894

Type species.—*Lituites praecurrens* Holm, 1891 from the Lower Ordovician (Kundan Stage) of Öland, Sweden.

Generic diagnosis.—Lituiticonic with adapically one-voluted gyroceraconic and adorally sigmoidal curved shell portion; septal necks orthochoanitic; surface ornamented with growth lines and annulations, forming ventral sinus and lateral salient in the earlier coiled stage and transverse or slightly undulating ones in the later stage.

Remarks.—Hyatt (1894) recognized that this genus is characterized by having distinct ventral and dorsal lobes in the ephebic stage, with low, broad, almost straight, lateral saddles.

Ancistroceras is most closely allied to *Holmiceras*, but differs from the latter in having small, tightly coiled whorls and a much more rapidly expanding conch. Sweet (1958) emphasized the sigmoid profile of the shell which is missing in *Ancistroceras*.

Holmiceras has long been an all-but-forgotten genus. However, Flower (1975) added *Holmiceras benetti* from the Middle Ordovician Table Head Formation in Newfoundland to the two previously known *Holmiceras* species. Presently, only four species in the world can be referred to *Holmiceras*; *Holmiceras praecurrens* (Holm, 1891), *Holmiceras kjerulfi*

(Brögger, 1882), *Holmiceras benetti* Flower, 1975 and *Holmiceras coreanicum* (Kobayashi, 1927) which is described below. *Holmiceras coreanicum* from the Jigunsan Formation is a first reliable record of this genus from Asia.

Holmiceras coreanicum (Kobayashi, 1927)

Figures 3-1a, b, 2a, b; 4-1-10.

Orthoceras coreanicum Kobayashi, 1927, p. 181, pl. 18, fig. 6; pl. 19, figs. 3a-c.

Orthoceras makkolense Kobayashi, 1927, p. 181, pl. 19, figs. 2a-c. *Sigmorthoceras coreanicum* (Kobayashi). Kobayashi, 1934, p. 413, pl. 22, fig. 7.

Sactorthoceras makkolense (Kobayashi). Kobayashi, 1934, p. 408, pl. 15, fig. 9.

Cycloceras sp. Kobayashi, 1934, p. 421, pl. 29, figs. 12, 13.

Sinuitopsis kochiriensis Kobayashi, 1934, p. 360, pl. 5, figs. 1-4. aff. *Trilacnoceras* sp. Ozaki and Ogino, 1968, pl. 3, fig. 3.

Holmiceras coreanicum (Kobayashi). Yun, 1998, p. 78, figs. 1c-h.

Types.—A sigmoidally curved phragmocone figured by Kobayashi (1927, p. 181, pl. 19, figs. 2a-c) from the Jigunsan Formation of Maggol, Kangweondo, Korea, UMUT PM9, is here designated as the lectotype (see also Figures 3-1a, b). A slightly curved phragmocone specimen from the same locality, UMUT PM8 is also designated as the lectoparatype.

Material.—In addition to the above two type specimens, newly collected specimens from the Jigunsan Formation including 9 figured (KPE20001, KPE20002, KPE20003, KPE20004, KPE20005, KPE20006, KPE20007, KPE20020, KPE20026-1, KPE20302) and 23 other specimens were

examined.

Specific diagnosis.—Sigmoidally curved conch with early loosely coiled portion; body chamber long; circular in cross section; siphuncular segments somewhat expanded within camera; septal necks orthochoanitic; no cameral deposits detected; surface ornamented with prominent annulations and very fine growth lines.

Description.—Conch large-sized lituiticone, composed of two different continuous shell portions, namely, early loosely coiled juvenile shell portion (Figures 4-1a-c—4) and later sigmoidally curved adult shell portion (Figures 4-6a, 7, 8).

The best preserved specimen, KPE20001 (Figures 4-1a—c), is broken into two portions, but when put together is about 63 mm long; the early juvenile shell portion is loosely coiled, its umbilical opening being 3.2 mm across, first camera pointed anterolaterally, constricted to 1 mm at a height of 1.5 mm from the adapical apex, forming a subquadrate outline; internal structure unknown owing to recrystallization; septa moderately concave and closely spaced with septal spacing 0.7 mm on the dorsum and 1 mm on the venter, gradually increasing adorally; slightly curved later shell portion, 58 mm long, circular in cross section, its diameter expanding from 7 mm at the adapical end to 15.7 mm at the broken upper end; siphuncle central, narrow, its width one-eighth of the conch diameter; siphuncular segments tubular to slightly inflated within camerae; transverse septal suture and surface annulations crossing each other; septal depth smaller than one cameral height on the concave side and larger than that on the convex side; cameral height gradually increasing towards the top from 1.3 mm to 2.9 mm, five camerae equal in length to the conch diameter of 15.9 mm measured at the uppermost camera; septal necks orthochoanitic, attaining 0.5 mm at the 3rd septum from the adoral end, occupying about one-third of the cameral height, distinguishable from the connecting ring by means of their thickness, septal suture transverse, but intersecting with annulations; camera filled with crystalline calcite, no organic deposits detected; siphuncle lined by endosiphuncular nonsegmental material along the inner siphuncular wall and leaving central narrow siphotube; surface ornamented with low, narrow annulations separated by much broader intergrooves, both of which are covered with very fine transverse growth lines, showing different features during ontogeny, ventral sinus and lateral salients in juvenile coiled stage and then adorally run parallel to transverse axis, 7 annulations in a length equal to the conch diameter at the preserved adoral end, annulation density slightly larger than that of septal one, i.e., 8 growth lines occurring between two annulations.

KPE20002 (Figure 4-4) represents a young, possibly embryonic or early postembryonic shell with 10 camerae consisting of endogastrically curved gyroconic phragmocone and subsequent straight body chamber, small, 15.5 mm long, conch diameter rapidly enlarging from 2.2 mm near the adapical end to 4.9 mm at the base of the living chamber; siphuncle central, its segments expanded within camerae, constricted at the septal necks; septal depth corresponding to one cameral height; siphuncle filled with imported matrix, camera filled with crystalline calcite; surface annulated in longitudinal section, being arranged at intervals of 0.8 mm.

KPE20003 (Figure 4-2) judging from the silicone rubber cast, is the external mould of an early coiled shell portion, 17.5 mm long, composed of a loosely coiled embryonic shell portion, its umbilical opening about 3 mm across, conch expanding at a rate of 1 mm per 4 mm; surface ornamented with prominent annulations and transverse fine growth lines, forming ventral and dorsal sinuses, and ventrolateral salients.

KPE 20004 (Figure 4-7), a sigmoidally curved phragmocone, 85.2 mm in length, conch diameter expanding moderately rapidly in the earlier stage from 3.8 mm to 10 mm at a distance of 21 mm and more slowly afterwards, conch circular in cross section; siphuncle narrow, central; septal necks orthochoanitic; cameral height ranging from 1.7 mm to 3 mm; septal depth slightly larger than one cameral height; surface ornamented with primary annulations and very fine growth lines.

KPE20005 (Figure 4-5) is a sigmoidally curved fragmentary phragmocone, 76 mm in length, conch diameter gently expanding from 10.2 mm at the adapical end to 22.9 mm at the adoral end; siphuncle subcentral, narrow, occupying one-seventh of the conch diameter; siphuncular segments slightly inflated within camera, dimensions 2.6 mm in length and 3 mm in maximum diameter at the midportion of the segment in the adoral end, constricted to 2.2 mm at the septal foramina; septal necks suborthochoanitic, septa relatively deep, exhibiting one and a half of the cameral height; septal distance varying from 1.9 mm to 2.8 mm; nonsegmental endosiphonal linings along the siphuncular wall, leaving a central tube; surface ornamented with distinct annulations and growth lines.

KPE20006 (Figure 4-10) is an external mould retaining well preserved surface ornamentation, consisting of annulations very closely spaced at intervals of approximately 1 mm, with ventral sinus formed by each annulus about 2.6 mm in width and about 1.3 mm in length in earlier shell portion, and of much more widely spaced, more prominent transverse annulations in later shell and further annulations again becoming narrower in gerontic shell, annulations and intergrooves both covered with very fine growth lines.

KPE20007 (Figures 4-6a, b) represented by a moderately curved, large-sized adult shell lacking an early coiled portion, is 162 mm long of which the body chamber is 57 mm long, adoral portion of phragmocone and body chamber secondarily depressed during fossilization, conch circular in cross section; its diameter gently enlarging from 19.7 mm at the adapical end to 33.3 mm at a point 74 mm farther up; siphuncle central, narrow, a little more than one-seventh of the conch diameter; siphuncular segment as long as broad; surface ornamentation on body chamber partly preserved, comprising annulations and growth lines.

KPE20302 (Figure 4-8), 53.5 mm in length, consists of a loosely coiled early shell portion and succeeding sigmoidally curved conch, but an initial chamber is not preserved; umbilical opening about 2.8 mm across; moderately expanding at a rate of 1 mm per 5 mm.

Remarks.—*Sigmorthoceras coreanicum* from the Jigunsan Formation of Maggol (Kobayashi, 1927, pl. 18, fig. 6; pl. 19, figs. 3a-c; 1934, p. 413, pl. 22, fig. 7) is the type species of *Sigmorthoceras* which has been regarded as a doubtful

taxon for a long time. Externally, the slightly curved conch was regarded as the diagnostic character by Kobayashi (1934). However, Shimizu and Obata (1935a) regarded the sigmoidal conch shape of specimens of *Sigmorthoceras* described by Kobayashi as a secondarily deformed *Sactorthoceras makkolense*. Such secondary deformation is common in other nautiloid fossils from this region. Flower (1946) stated that *Sigmorthoceras* is an erratic form deviation, perhaps not worthy of generic status.

However, the internal morphology of the sigmoidally curved conch of the present species is identical with that of the type specimens of *Sigmorthoceras coreanicum*. Based on the identical curvature of all the specimens, the secondary deformation conjecture by Shimizu and Obata (1935a) can be rejected. Thus, *Holmiceras coreanicum* is revealed to possess a loosely coiled early shell portion and slightly sigmoidal more mature conch.

It is well known that secondary deformation and dissolution of shelly matter during fossilization sometimes cause misidentification of fossil taxa. Kobayashi (1934) described *Cycloceras* sp. from the Jigunsan Formation of Homyeong (p. 421, pl. 29, figs. 12, 13), based on the annulated ornamentation. The annulations observed on the ventral portion near the adapical end of the specimen are more broadly spaced than those on the dorsal one. Accordingly, the specimen represents a portion of the shell shifting from the early coiled stage to the sigmoidally curved phragmocone in *Holmiceras coreanicum*. Furthermore, all the features observed in the longitudinal section agree well with those of *Holmiceras coreanicum*, although the state of preservation of the internal structure is rather poor.

Meanwhile, Kobayashi (1934) described a sinuitid gastropod, *Sinuitopsis kochiriensis* from the Jigunsan Formation of Homyeong, based on two incomplete external moulds (Kobayashi, 1934, p. 360, pl. 5, figs. 1–4). In general, the genus *Sinuitopsis* consists of a tightly coiled shell with 3 to 4 volutions (Knight *et al.*, 1960, pl. 176, fig. 93–7a, b) and its surface is sculptured by fine growth lines without more raised primary annulations. However, the specimens described by Kobayashi (1934) as "*Sinuitopsis*" have loosely coiled shells having one volution and lacking the characteristic surface sculpture of true *Sinuitopsis*. In addition, its surface ornamentation consisting of ventral sinus and lateral salients is strong evidence to support the contention that the two external moulds belong to *Holmiceras*.

Sactorthoceras makkolense (Kobayashi, 1927) was proposed based on two individuals. One of them (UMUT PM7; Figures 3–2a, b), illustrated in Kobayashi (1927, pl. 19, figs. 2a–c) differs from the other specimen (UMUT PM6; Kobayashi, 1927, pl. 18, fig. 5; see also Figures 3–4a, b) in having more crowded septa and a narrower siphuncle.

Accordingly, the former specimen (UMUT PM7) is dissimilar to the lectotype but has a cameral height of no more than two-thirds the diameter of the siphuncle. Moreover, the conch of the specimen has a slightly curved form, although its siphuncular position is more or less eccentric due to secondary deformation. In these respects, this specimen must also be assigned to *Holmiceras coreanicum*.

Ozaki and Ogino (1968, pl. 3, fig. 3) figured a single nautiloid, aff. *Trilacinceras* sp. from the Jigunsan Formation of Dongjeom. It is represented by an early coiled phragmocone. However, its generic identification may be incorrect because of the less loosely coiled portion of the conch than those in the species of the genus *Trilacinceras*. Based on the mode of coiling in the early portion of the conch and the surface ornamentation, this nautiloid is assigned with reservation to *Holmiceras coreanicum*.

Comparison.—In view of the external morphology, this species is closely allied to *Holmiceras kjerulfi* (Brögger) from the *Orthoceras* Limestone of the Oslo region, Norway (Brögger, 1882, p. 54, pl. 12, fig. 16), but differs from the latter species by its loosely gyroceratonic volution, somewhat curved cyrtoconic or sigmoidal adoral portion, circular section of the conch and slightly more crowded septa. This species is distinguished from *Holmiceras benetti* Flower from the Middle Ordovician Lower Table Head Limestone, Newfoundland (Flower, 1975, p. 151, pl. 4, figs. 1–6), which has a more rapidly expanding conch and lacks a sigmoidal adoral shell portion.

This species is similar to the Middle Ordovician species *Ancistroceras undulatum* Boll, 1857 recovered from erratic boulders in northern Germany (Foerste, 1929, p. 272, pl. 41, figs. 3, 4) and the Ampyx Limestone in Oslo-Asker district, Norway (Sweet, 1958, p. 129, pl. 13, figs. 2, 3, 5) in that the early coiled portion and the mode of surface ornamentation are similar to *H. coreanicum*, but this taxon is quite distinct from the latter in its more slowly expanding conch. Likewise, *Ancistroceras subcurvatum* Qi, 1980 from the upper Taiwan Formation, Lower Ordovician, Wuwei, Anhui, China (Qi, 1980, p. 256, pl. 1, figs. 1, 2) is similar to this species in general features but also differs from it by its own somewhat more rapidly expanding conch.

Occurrence.—This species is known to occur from various localities (SN801, SN802, SN809, SN835, DJ500 and MH201) in the Middle Ordovician Jigunsan Formation.

Order Orthocerida

Family Sactorthoceratidae

Genus *Sactorthoceras* Kobayashi, 1934

Type species.—*Sactorthoceras gonioseptum* Kobayashi, 1934 from the Jigunsan Formation of Maggol, Kangweondo, Korea.

→ **Figure 3.** 1a, b, 2a, b. *Holmiceras coreanicum* (Kobayashi, 1927). 1a, b. A sigmoidally curved phragmocone, lectotype (UMUT PM9), $\times 1$, 1a: lateral view, 1b: longitudinal section. 2a, b. "*Sactorthoceras makkolense* (Kobayashi)", UMUT PM7, which is here assigned to *Holmiceras coreanicum* (Kobayashi), $\times 1$, 2a: lateral view, 2b: longitudinal section. 3a, b. *Kotoceras grabau* (Kobayashi, 1927). The best preserved partial phragmocone, lectotype (UMUT PM631), $\times 1$, 3a: ventral view, 3b. adoral view of the septa and siphuncle, venter down. 4a, b. *Sactorthoceras makkolense* (Kobayashi, 1927). An adoral phragmocone, lectotype (UMUT PM6), 4a: longitudinal section, $\times 1$, 4b: enlargement of the same section, $\times 2$.



1a



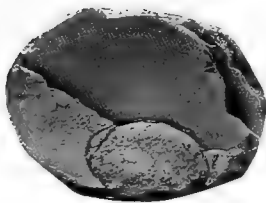
1b



2b



2a



3b



3a



4a



4b

Generic diagnosis.—Straight or slightly curved longiconic orthoceracone with subcentral siphuncle; siphuncular segments tubular or slightly expanded within camerae; cameral height nearly equal to or a little more than siphuncular diameter; no discernible cameral and endosiphuncular deposits; surface smooth or ornamented with closely spaced annulations and very fine transverse growth lines.

Remarks.—The genus *Sactorthoceras* is known from the Middle Ordovician formations in East Asia, Norway and northeastern America. Flower (1941) considered *Sactorthoceras* as the ancestor of the ascocerid nautiloids that make up a specialized group having siphuncular segments from orthochoanitic to cyrtochoanitic.

Indeed, *Sactorthoceras* may be not distinguished from *Holmiceras* when any specimen is found as an adoral broken phragmocone without an early coiled shell portion. However, the longitudinal section through the center of the siphuncle reveals that the siphuncle of *Sactorthoceras* is always broader and its septal distance is higher than in *Holmiceras*.

The generic assignment of *Cycloceras* M'Coy is based mainly on the surface ornamentation and not on internal structure. The Group 1 of *Cycloceras* which was divided artificially by Kobayashi (1934) is regarded as belonging to either *Sactorthoceras* or *Holmiceras*, because its internal structure and surface ornamentation agree well with the latter genera. Moreover, Sweet (1964) mentioned that "no species other than the type species should be referred to *Cycloceras* until its type is better known". Based on present knowledge, the genus *Cycloceras* may be superseded by *Wenianoceras*, which was proposed by Chen (1976) for shells having a strongly annulated surface and a central siphuncle.

Sactorthoceras makkolense (Kobayashi, 1927)

Figures 3-4a, b; 5-1-6; 6-1-4

Orthoceras makkolense Kobayashi, 1927, p. 181, pl. 18, fig. 5; not pl. 19, figs. 2a-c.

Sigmothoceras sigmoidale Kobayashi, 1934, p. 414, pl. 21, figs. 1-3.

Sactorthoceras gonioseptum Kobayashi, 1934, p. 412, pl. 16, fig. 6; pl. 18, figs. 1-3; pl. 20, fig. 9.

Sactorthoceras shimamurai Kobayashi, 1934, p. 408, pl. 19, figs. 1

3.

Kawasakiceras densistriatum Kobayashi, 1934, p. 397, pl. 14, figs. 6, 7.

Cycloceras taihakuense Kobayashi, 1934, p. 420, pl. 22, figs. 1, 2; pl. 23, figs. 1-5; pl. 24, figs. 4-6.

Sactorthoceras makkolense (Kobayashi). Kim *et al.*, 1986, p. 26, pl. 6, figs. 1, 2.

Type.—The type specimen, UMUT PM6, from the Jigun-san Formation of Maggol, Kangweondo, Korea is here designated as the lectotype (Figures 3-4a, b).

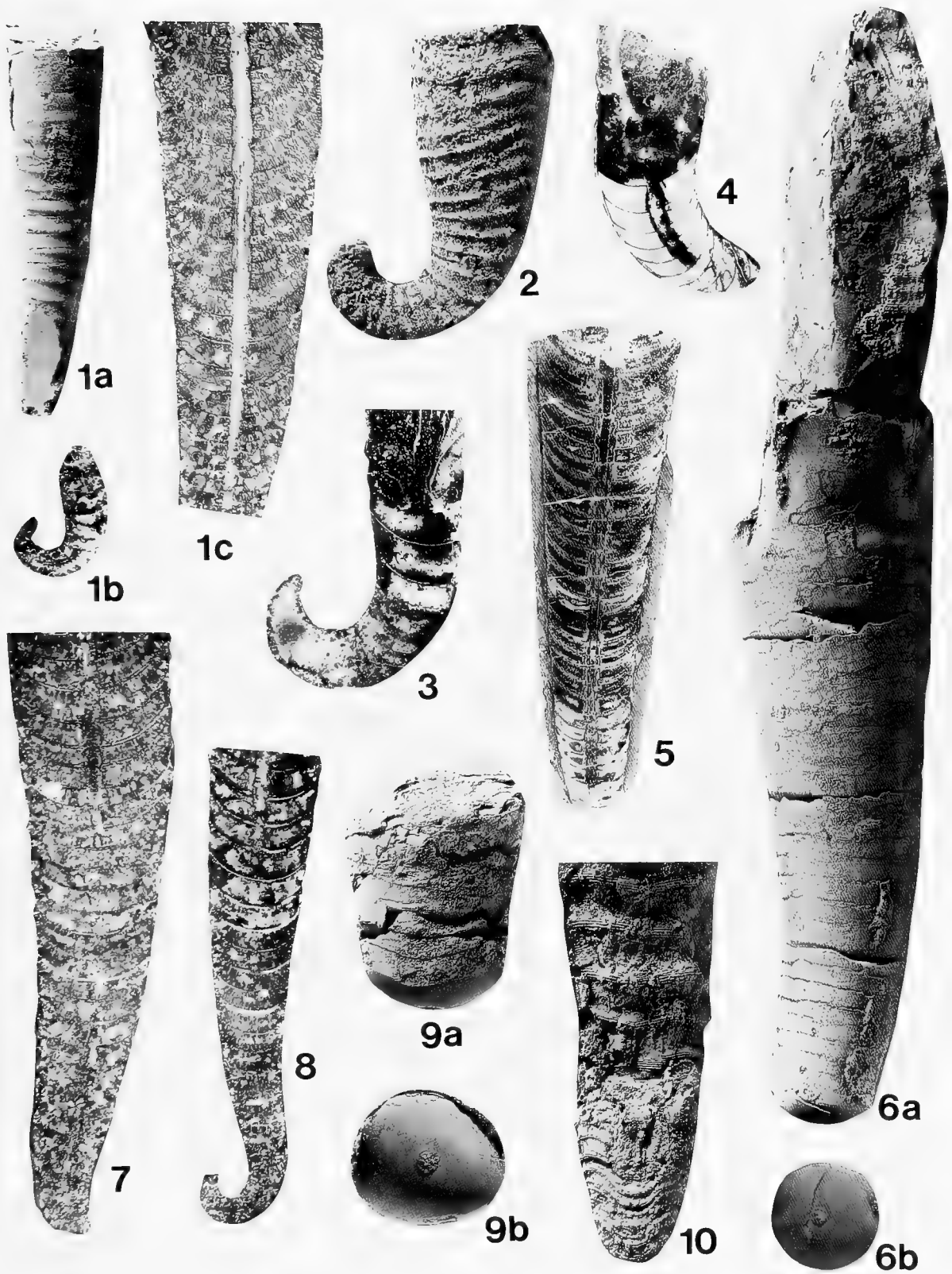
Material.—15 specimens including seven figured ones (KPE20030, KPE20031, KPE20032, KPE20033, KPE20036, KPE20037, UMUT PM634).

Specific diagnosis.—Longiconic orthoceracone; siphuncular segments tubular; septal necks orthochoanitic to suborthochoanitic; cameral height nearly equal to siphuncular diameter; surface ornamented with low annulations and very fine transverse growth lines.

Description.—Conch large-sized longiconic orthoceracone, enlarging at a rate of 1 mm per 8 to 10 mm in conch length; cross sections of conch and siphuncle subcircular; ratio of the siphuncular diameter versus conch diameter being 1:9 in KPE20030 (Figure 5-3); siphuncle subcentral, tubular; septa moderately concave forwards, septal depth nearly two to three times the cameral height, septal distance ranging from 3.3 mm to 5.4 mm, in other words, a little more than or equal to the siphuncular diameter, septal necks orthochoanitic, relatively long, approximately 2 mm in KPE20037 (Figure 5-6), bending smoothly toward adapical end and then forming a right angle with septa, septal suture directly transverse; connecting ring thin, distinguishable from septal neck by its thickness; in KPE20037 camerae comparatively high, ranging from 3.5 mm to 4 mm, 7 to 8 camerae in a distance corresponding to the conch diameter; no cameral or siphuncular deposits detected; surface marked with low, narrow annulations, separated by broader interspaces, both covered with very fine numerous transverse growth lines, 7 to 8 per 1 mm length, annulations being arranged at intervals of about 2 mm, but fluctuating within a narrow range.

Remarks.—Kobayashi (1927) described the present species as follows: "In the middle part of the polished specimen (pl. XVIII, fig. 5) the segmentation is quite abnormal, the double

→ **Figure 4.** *Holmiceras coreanicum* (Kobayashi, 1927). **1a c.** Partial phragmocone steinkern (KPE20001) from SN801, **1a**: ventrolateral view, showing the septal suture crossing annulations, $\times 1$, **1b**: dorsoventral section of coiled embryonic conch, $\times 1.3$, **1c**: longitudinal section of partial phragmocone made by an acetate peel, showing the details of siphuncle and septa, $\times 1.5$. **2.** Silicon rubber cast of external mould (KPE20003) from DJ500, showing loosely coiled embryonic shell portion with annulated surface ornamentation, $\times 3$. **3.** Juvenile shell (KPE20026-1) from MG343, dorsoventral section of the early coiled septated shell portion, $\times 3$. **4.** Possibly embryonic conch (KPE20002) from SN801, dorsoventral section, showing the phragmocone and subsequent body chamber, $\times 3$. **5.** Partial phragmocone (KPE20005) from DJ500, longitudinal section, showing details of siphuncle and septa, $\times 1$. **6a, b.** Moderately curved conch (KPE20007) from SN801, $\times 1$. **6a**: lateral view. Surface ornamentation is partly preserved on body chamber. **6b**: apical view, showing the position of the siphuncle. **7.** Longitudinal section of partial phragmocone (KPE20004) from SN801 made by an acetate peel, showing the sigmoidally curved conch and details of siphuncle and septa, $\times 2$. **8.** Early coiled and later sigmoidally curved conch (KPE20302) from SN802, $\times 1.5$. **9a, b.** Partial phragmocone (KPE20020) from SN801, $\times 1$, **9a**: lateral view, **9b**: apical view of septum and siphuncle, showing the position of siphuncle. **10.** Partial phragmocone (KPE20006) from DJ500, ventral view, silicon rubber cast of external mould, showing the well developed surface ornamentation, especially ventral sinus of annulations on earlier portion, $\times 2.5$.



camerae on one side of the siphuncle corresponding to a single camera on the other. It may be possibly be due to a pathological state". However, in the type specimens of this species (Figures 3–4a, b), the septa in the adoral portion of the phragmocone are distributed disorderly here and there. This peculiar shell feature is considered to be an artifact created by recrystallization. As the result of restoration, the septa on each side in the each longitudinal section of the lectotype (UMUT PM6) correspond well one to one. This phenomenon is easily found in many cephalopods. For example, *Actinoceras bellefontense* Foerste and Teichert, 1930 shows a disagreement between septa on both sides owing to the diagenesis of internal components (Foerste and Teichert, 1930, p. 227, pl. 38, fig. 2B). Stridsberg (1990) suggested that internal destruction of septa may be caused by implosion due to increasing water pressure during post-mortem sinking. Accordingly, the abnormal camerae observed in the lectotype of *Sactorthoceras makkolense* may not represent a pathological state during life, but were formed secondarily by taphonomic processes.

Taphonomic damage gave rise to other taxonomic problems too. Kobayashi (1934, p. 408, pl. 19, figs. 1–3) proposed *Sactorthoceras shimamurai* for a specimen with very rapid expansion of the conch, namely, at the rate of 1 mm per conch length of 4 mm. However, this specimen (UMUT PM643), which is represented by a fragmentary phragmocone with the last six camerae being closely spaced and a strongly compressed, large-sized body chamber, does not reflect the real expansion rate of the shell owing to secondary deformation of the body chamber and erosion of one side. Furthermore, since the last six camerae indicate the gerontic stage, more widely spaced camerae would be present in the adolescent stage. Consequently, *Sactorthoceras shimamurai* is regarded as a junior synonym of *Sactorthoceras makkolense*.

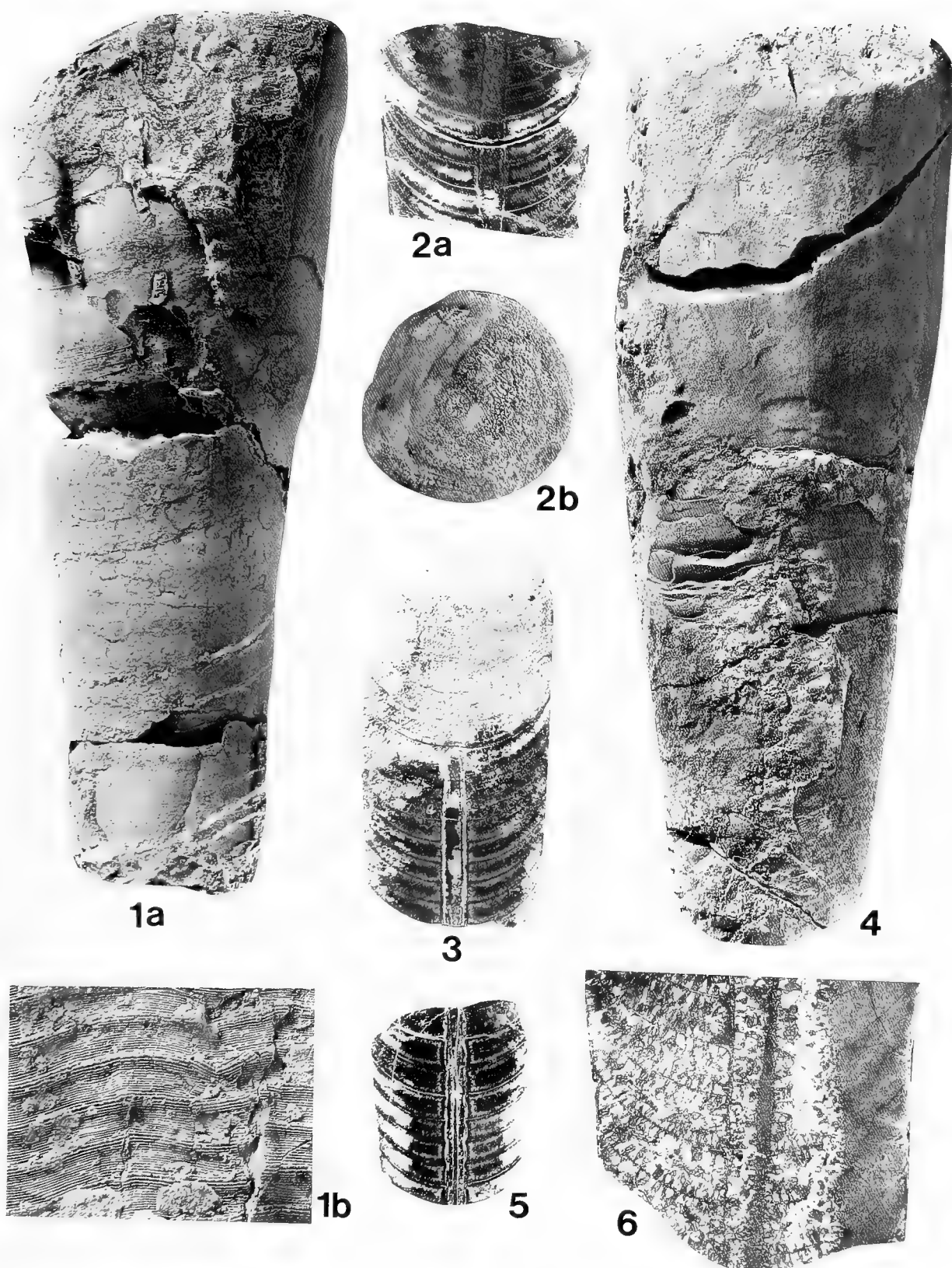
Sactorthoceras gonioseptum from the Jigunsan Formation of Maggol was described by Kobayashi (1934) as having a narrower siphuncle and more crowded septa than *Sactorthoceras makkolense*. He also emphasized the angulation of the septa shown in the holotype (UMUT PM650) as a diagnostic character of this species. However, this feature can not be observed in the specimen because of the crushed and distorted condition of the septa along the outer part of the cameral portion. Shell breakage during fossilization resulted in a pinched septal foramen with curiously angulated septal necks. Apart from the aberrant feature of septal angulation, *Sactorthoceras gonioseptum* can be regarded as a junior synonym of *Sactorthoceras makkolense*.

Kobayashi (1934) established *Sigmorthoceras sigmoidale* on the basis of a single sigmoidally curved specimen (UMUT

PM652). He stated that this species is characterized by more broadly spaced septa and a broader siphuncle than in *Sigmorthoceras coreanicum*. Kobayashi (1934) described the shell surface of this specimen as smooth, but reanalysis of the same specimen revealed that it is actually sculptured by weak annulations and very fine transverse growth lines. Kobayashi (1934) emphasized that this species is closely similar to *Sactorthoceras makkolense*, except for the sigmoidal curvature of the conch. However, as Shimizu and Obata (1935a) pointed out, the sigmoidal mode of nautiloids from the Jigunsan Formation including *Sigmocycloceras kogenense* (Kobayashi), presumably originated by secondary deformation rather than from biological causes. Re-analysis of this specimen in longitudinal section indicates that over half of the right cameral portion is abraded and worn away and subsequently the chambers were filled with sediment. Therefore, this specimen probably suffered some secondary deformation from one side. It seems likely that this force together with compactional load changed this specimen to a sigmoidal form. Thus, the original morphological features of the type specimen of Kobayashi's *Sigmorthoceras sigmoidale* are identified with those of *Sactorthoceras makkolense*, indicating that the former species is a junior synonym of the latter.

Meanwhile, Kobayashi (1934) established *Kawasakiceras densistriatum* on the basis of its characteristic annulated and striated ornamentation on the surface. In the holotype (UMUT PM634), the large-sized ventral endosiphuncle which is a primary morphologic feature for the endoceroid nautiloids such as *Kotoceras* can not be detected. Re-examination of the specimen strongly suggests that Kobayashi mistakenly interpreted the fracture line through the center as holochanitic septal necks in his retouched figure in longitudinal section with a body chamber (Kobayashi, 1934, pl. 14, fig. 7; see also Figure 6). The right-half portion of the longitudinally sectioned type specimen may have been regarded as a ventral siphuncle. Also, the endocone which is the vacant space formed by the last endosheath is not observed in the portion that was considered by Kobayashi (1934) as the siphuncle. Therefore the septa are extended to the ventral margin and continue to the right-half portion. This fact is revealed not only by the preserved successive septa in longitudinal section but also by the camerae exposed on the lateral side of the specimen. In this way, this longitudinally sectioned specimen appears to represent a remaining part through which the siphuncle does not pass. Unfortunately, the other half is missing. It is evident that *Kawasakiceras densistriatum* does not possess a large ventral siphuncle as in the species of *Kotoceras*, but has a centrally located narrow siphuncle. In addition, the surface

→ **Figure 5.** *Sactorthoceras makkolense* (Kobayashi, 1927). **1a, b.** Partial phragmocone (KPE20036) from SN835, **1a**: lateral view, $\times 1$, **1b**: details of surface ornamentation, showing the annulations and fine growth lines, $\times 5$. **2a, b.** Fragmentary phragmocone (KPE20032) from DJ500, **2a**: longitudinal section, showing the siphuncle and septa, $\times 1$, **2b**: septal view, venter down, showing the position of the siphuncle, $\times 1$. **3.** Naturally weathered phragmocone (KPE20030) from DJ500, longitudinally polished section, $\times 1$. **4.** Incomplete large conch (KPE20033) from SN835, lateral view of partial conch, showing the phragmocone and subsequent body chamber, $\times 1$. **5.** Partial phragmocone (KPE20031) from DJ500, longitudinal section, showing the slightly inflated siphuncular segments, $\times 1$. **6.** Partial phragmocone (KPE20037) from SN809, longitudinal section, showing the internal cameral structure, $\times 1$.



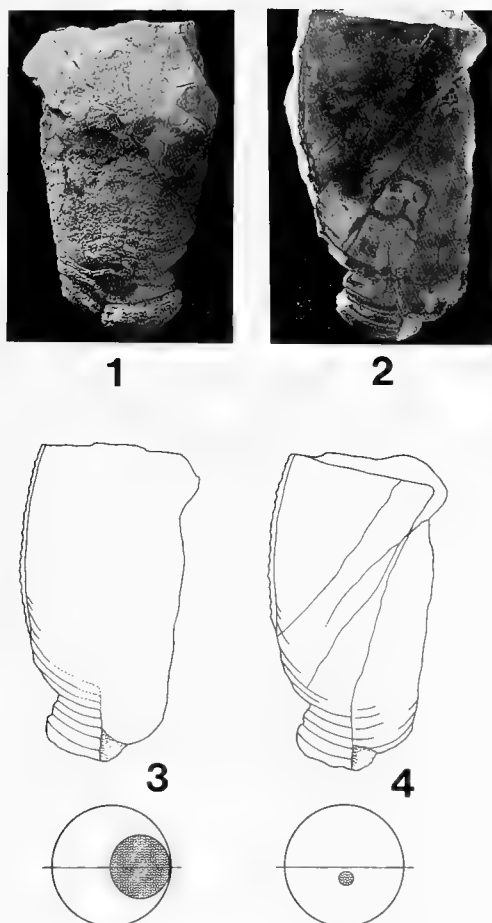


Figure 6. "*Kawasakiceras densistriatum* Kobayashi", UMUT PM634, which is here assigned to *Sactorthoceras makkolense* (Kobayashi). **1.** Lateral view, $\times 0.5$. **2.** Longitudinal section, $\times 0.5$. **3.** Sketch based on Kobayashi's view, showing the broad ventral siphuncle. **4.** Sketch based on reexamination of the holotype, showing the septa instead of siphuncle. Longitudinal (upper) and cross (lower) sections are shown in **3** and **4**.

ornamentation agrees well with the pattern of the species of *Sactorthoceras*. Accordingly, this species is attributed to *Sactorthoceras makkolense* (Kobayashi, 1927), based on the moderately concave septa, probably central narrow siphuncle and annulated surface ornamentation with a fine transverse striation.

Comparison.—This species is similar to *Sactorthoceras wongiforme* Kobayashi from the Jigunsan Formation of Maggol and Hwangjiri (Kobayashi, 1934, p. 410, pl. 20, fig. 10; pl. 31, figs. 1, 2) in its tubular siphuncle and moderately concave septa, but differs from the latter in its broader siphuncle and higher camera.

Sactorthoceras tenuicurvatum Kobayashi from the Jigunsan Formation of Homyeong and Sanaegol (Kobayashi, 1934, p. 409, pl. 16, figs. 1, 2; pl. 17, figs. 9, 10) is readily distinguished from this species by its gentle curvature and ellipti-

cal section of the compressed conch.

This species resembles *Sactorthoceras* sp. from the Cephalopod Shale at Hovindsholm, Helgøya, Oslo region, Norway (Sweet, 1958, p. 60, pl. 3, fig. 12; pl. 4, figs. 1, 7), but its septal concavity is nearly three times of cameral height, while that of the latter species is less than half the length of a camera.

Occurrence.—Rarely occurs at the localities SN802, SN809, SN835, and DJ500 in the Middle Ordovician Jigunsan Formation.

Subclass Endoceratoidea
Order Endocerida
Family Endoceratidae
Genus ***Kotoceras*** Kobayashi, 1934

Type species.—*Kotoceras typicum* Kobayashi, 1934 from the Jigunsan Formation of Maggol.

Generic diagnosis.—Longiconic or somewhat curved orthoceracone, subcircular to ovate in cross section; siphuncle marginal, broad, nearly a half of the dorsoventral conch diameter or less, in actual contact with slightly flattened ventral wall; endocones extending much farther forward ventrally than on dorsal side, apical end slightly closer to the dorsal side than the ventral one; septal necks holochoanitic; suture disconnected at ventral flattening; surface smooth.

Remarks.—*Kotoceras* is one of the Asiatic endemic genera from the Jigunsan Formation, Korea, and several species of the genus are known from China and Siberia. The diagnostic generic characters are the asymmetric endosiphoncone and the disconnected septal suture on the ventral side. Kobayashi (1934) emphasized that *Kotoceras* is easily distinguished from other related genera, *Endoceras*, *Vaginoceras*, and *Cameroceras* in having the marginal siphuncle in actual contact with the shell wall on the broadly flattened venter. Flower (1958) recognized that his *Lamottoceras* is very similar to the Asiatic *Kotoceras*, in which holochoanitic septal necks are present. However, the genus *Lamottoceras* differs from *Kotoceras* in having aneuchoanitic septal necks and thick connecting rings.

Kotoceras grabau (Kobayashi, 1927)

Figures 3-3a, b; 7-1—4; 8-1—4

Vaginoceras grabau Kobayashi, 1927, p. 79, pl. 18, figs. 1a-c, 2. *Vaginoceras frechi* Kobayashi, 1927, p. 179, pl. 18, figs. 2a-c. *Kotoceras grabau* (Kobayashi). Kobayashi, 1934, p. 395, pl. 11, figs. 5-8; pl. 12, fig. 6; pl. 14, figs. 5-8. *Kotoceras frechi* (Kobayashi). Kobayashi, 1934, p. 395 (not figured).

Type.—The best preserved and largest specimen (UMUT PM631) is designated here as the lectotype of *Kotoceras grabau* (Kobayashi) (Figures 3-3a, b).

Material.—Eleven specimens including the five figured ones (KPE20042, KPE20043, KPE20044, KPE20045, UMUT PM3).

Specific diagnosis.—Subcircular to elliptical in cross sec-

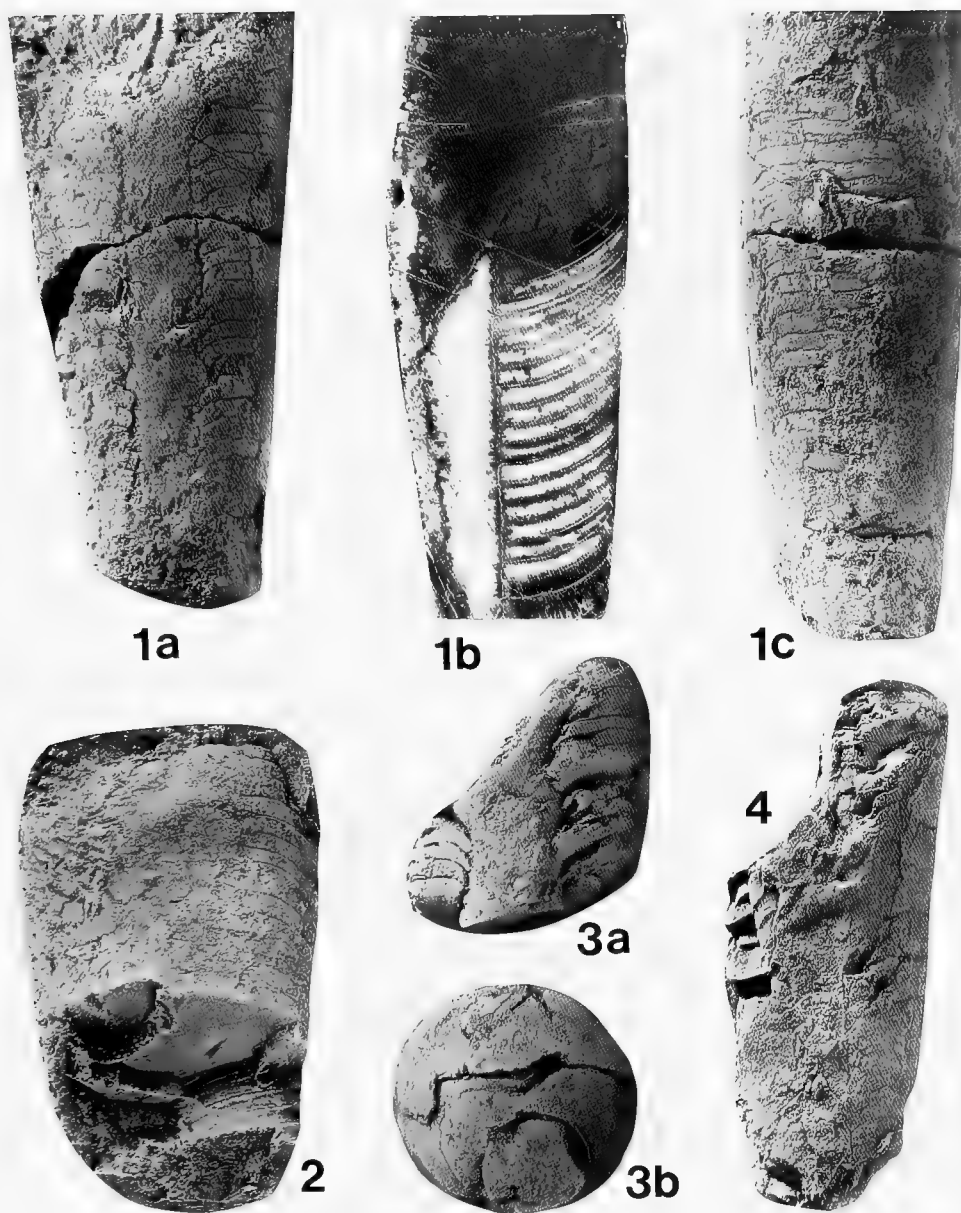


Figure 7. *Kotoceras grabaui* (Kobayashi, 1927). **1a-c.** Partial phragmocone (KPE20042) from SS663, $\times 1$, **1a**: ventral view, showing the disconnected septal suture, **1b**: dorsoventral section, venter on left, showing the large siphuncle with endosiphuncular deposits and closely spaced septa, **1c**: lateral view, venter on left side, showing the transverse septal suture. **2.** Strongly compressed phragmocone (KPE20043) from MG350, dorsolateral view, venter on right, showing the septal neck impressions on ventral side of the siphuncle, $\times 1$. **3a, b.** Partial phragmocone (KPE20044) from MG357, $\times 1$, **3a**: ventral view, showing the siphuncle-septal neck portion, **3b**: apical view of septum and siphuncle, showing the nearly circular conch cross section and slightly depressed siphuncle. **4.** Partial phragmocone (KPE20045) from MG357, ventral view, showing the somewhat flattened ventral side, $\times 1$.

tion; septal suture transverse, but gradually bends adapically and then turns into longitudinal section; septal impressions sloping from venter to dorsal; siphuncle large, nearly half or a little less than half the dorsoventral conch diameter; camerae crowded.

Description.—Conch medium-sized longiconic orthoceracone, represented by several fragmentary phragmocones, its diameter gently enlarging at a rate of 1 mm per conch length of 9 mm in KPE20045 (Figure 7-4); conch elliptically ovate to subcircular in cross section, slightly dorsoventrally

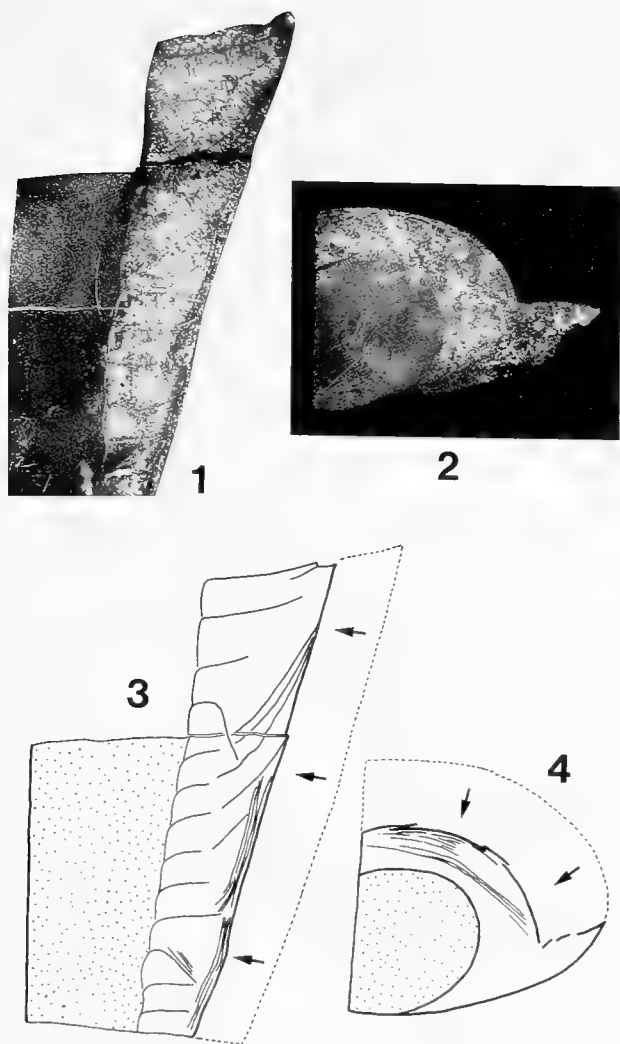


Figure 8. "*Kotoceras frechi* (Kobayashi)", UMUT PM3, which is here assigned to *Kotoceras grabau* (Kobayashi). **1.** Longitudinal section shown by an acetate peel, $\times 2$. **2.** Cross section by the same method, $\times 2$. **3, 4.** Sketches of longitudinal section and cross section, respectively, showing the strongly depressed cameral portion and broken septa. Arrows indicate the direction of compaction.

depressed, ratio of the dorsoventral to lateral diameter of the conch near the adoral portion being 7:8 in KPE20042 (Figure 7-1); siphuncle marginal, in actual contact with the ventral wall, its cross section elliptical to subcircular, ventrally more flattened, expansion rate of the siphuncle commensurate with that of the conch; septal impression on the siphuncle running obliquely down from ventral to dorsal, its distance being about 2 mm or more in KPE20043 (Figure 7-2); camerae crowded, averaging 11 in the distance of the dorsoventral diameter of the conch, tending to broaden adorally in the middle part of the phragmocone, but finally attaining a height of 1.5 mm in KPE20042 (Figure 7-1); septal necks holochaoanitic; septa moderately concave adorally,

their depth corresponding to one and a half times the cameral height, increasing adorally where attaining a little more than twice the cameral height; septal ridge on the siphuncle running obliquely from ventral to dorsal; septal suture laterally transverse, but dorsally abruptly inclined backward, gradually bending posteriorly on the ventral side, and then becoming parallel to vertical axis; no endocone observed; camera filled with clastic sediments; surface apparently smooth.

Remarks.—Kobayashi (1927) proposed *Vaginoceras frechi* from the Jigunsan Formation of Maggol, based on a single specimen (p. 179, pl. 18, figs. 2a-c; UMUT PM3; Figure 8). Kobayashi (1934) subsequently reassigned this species to *Kotoceras*. According to his description, the characteristics of this species are summarized as follows: "The septum is gently inclined near the siphuncle but very steeply near the shell wall and is subangulated at a point where the septum bends from a gentle to a sharp angle". Kobayashi (1934) mentioned that this species is distinguished from *Kotoceras typicum* by having a more rapidly expanded conch, broader siphuncle and more concave septa.

However, the monotype of this species, UMUT PM3, is secondarily deformed along the dorsal margin, so that the above features may not fairly represent the specific diagnosis (Figure 8). Firstly, in the longitudinal section, septa of the dorsal portion are crushed by depression and then three or four septa are duplicated so as to be obliquely parallel with the shell wall. Most of the septa on the dorsal margin are irregularly arranged and broken. Because the clusters of broken septa are piled up longitudinally along the dorsal wall, the degree of convexity of each septum appears to change abruptly at a point midway on the septa. Secondly, the siphuncle has an unusually large diameter as compared with the conch diameter. In every species of *Kotoceras*, the siphuncle generally takes up one-third to a half of the conch diameter. The cameral portion in *Kotoceras frechi* is only one-third. The appearance must have been deformed by the effect suffered from sediments outside the dorsal portion. Thus, the diagnostic features of the specimen described as *Kotoceras frechi* by Kobayashi (1927, 1934) may be the result of diagenetic deformation, and therefore this taxon can be reassigned as a junior synonym of *Kotoceras grabau* (Kobayashi, 1927).

In the meantime, Chen and Zou (1984, p. 80, pl. 16, fig. 6) identified a longitudinally sectioned specimen from the Lower Ordovician Yaodian Formation of Shaanxi, North China as *Kotoceras frechi*. However, this specimen is assignable to *Kotoceras multiseptum* Kobayashi from the Jigunsan Formation of Maggol in having crowded and deeply concave septa and a broad siphuncle.

Comparison.—This species is comparable to *Kotoceras stolbovense* Balashov from the Middle Ordovician Krivolutsky Formation of the Siberian Platform (Balashov, 1962, p. 32, pl. 26, figs. 1a-d); however, the present species has a much shallower septal concavity and slightly larger siphuncle.

Kotoceras typicum Kobayashi from the Jigunsan Formation of Maggol (Kobayashi, 1934, p. 392, pl. 11, figs. 1-4) is distinguished from *K. grabau* by its more broadly spaced septa, nearly circular cross section of the conch in juvenile shell,

and shell surface with fine growth lines.

In the septal distance and the shape of the cross section, *Kotoceras multiseptum* Kobayashi from the Jigunsan Formation of Maggol (Kobayashi, 1934, p. 394, pl. 12, figs. 1, 2; pl. 13, figs. 1-3) is closely allied to *K. grabau*, but its conch expansion rate is much more rapid than that of the latter. *Kotoceras cylindricum* Kobayashi from the Jigunsan Formations of Maggol and Homyeong (Kobayashi, 1934, p. 393, pl. 12, figs. 7-9; pl. 13, figs. 8, 9) is easily distinguished from *K. grabau* by its circular cross section with a depressed siphuncle and more crowded septa.

Occurrence.—Middle Ordovician Jigunsan Formation, localities; SR900, SS663, MG343, MG350 and MG357.

Acknowledgments

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***Esgueiria futabensis* sp. nov., a new angiosperm flower from the Upper Cretaceous (lower Coniacian) of northeastern Honshu, Japan**

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Abstract. Bulk sieving of samples from the Ashizawa Formation, Futaba Group (lower Coniacian) of northeastern Honshu, Japan, has yielded a well-preserved plant mesofossil assemblage comparable to those recently described from eastern North America, Europe and central Asia. The most distinctive component of the assemblage is a new species of the genus *Esgueiria* (*Esgueiria futabensis* sp. nov.), a fossil flower known previously only from the Upper Cretaceous (Campanian–Maastrichtian) of Portugal. A possible additional species of the genus has also been recovered from a second mesofossil assemblage in the Tamayama Formation (lower Santonian). The occurrence of *Esgueiria* in Europe and eastern Asia during the Late Cretaceous indicates that despite the vegetational differences between these areas inferred from fossil pollen, some elements were widespread across middle paleolatitudes, presaging the strong floristic similarities among mid- and high latitude regions of the Northern Hemisphere during the early Tertiary.

Key words : Angiosperm flower, Ashizawa Formation, Coniacian, *Esgueiria futabensis* sp. nov., Santonian, Tamayama Formation

Introduction

Studies of the early fossil history of flowering plants (angiosperms) have been revolutionized over the last 15 years by the discovery of abundant, small, well-preserved and systematically informative fossil flowers in assemblages of Cretaceous plant mesofossils from Europe and eastern North America (e.g., Friis and Skarby, 1982; Friis, 1983; Knobloch and Mai, 1984; Friis *et al.*, 1994; Crane *et al.*, 1994). These specimens have yielded important information relating to the early diversification of many lineages of extant angiosperms and the evolution of their pollination and dispersal biology (e.g., Crane *et al.*, 1995). Only recently have similar mesofossil assemblages been recognized in central Asia (Frumina *et al.*, 1995; Frumina and Friis, 1996, 1999), and we now report that they also occur in eastern Asia. In this paper we describe the most characteristic of several fossil flowers in newly discovered plant mesofossil assemblages from the Futaba Group (lower Coniacian–lower Santonian) of Northeast Japan.

Materials and methods

Plant fossils were isolated from two sets of bulk samples collected at two different levels in the Futaba Group exposed in Fukushima Prefecture, northeastern Honshu, Japan. The fossils are small, three-dimensional and charcoallified or lignitized mesofossils. The Kamikitaba plant mesofossil assemblage (sample F16) was isolated from a poorly sorted, carbonaceous, black, sandy siltstone collected along a tributary of the Kitaba River in Kamikitaba, Hirono-machi (Study Route B of Ando *et al.*, 1995; 37°12'N, 140°57'E). These samples were from the Asamigawa Member of the Ashizawa Formation, which is interpreted as alluvial fan sediments (Ando, 1997). The Kohisa plant mesofossil assemblage (sample F11), comprised a poorly sorted, beige, sandy siltstone with scattered carbonaceous flecks. It was collected along the Kohisa River, Kohisa, Ouhisa-machi northeast of Iwaki City (Study Route N of Ando *et al.*, 1995; 37°10'N, 140°57'E). These samples were from the middle part of the Tamayama Formation, which is interpreted as braided river flood plain sediments with lagoonal facies in the uppermost part (Ando, 1997).

The Futaba Group comprises fluvial to shallow marine

sediments in the southern Abukuma Belt of Northeast Japan (Ando *et al.*, 1995). The Ashizawa Formation is the lowermost formation in the Futaba Group, and is overlain by the Kasamatsu Formation, which itself is overlain by the Tamayama Formation. Based on the occurrence of lower Coniacian ammonites and inoceramids in the middle of the Ashizawa Formation, and a lower Santonian inoceramid (*Inoceramus amakusensis*) in the upper part of the Tamayama Formation, the Futaba Group is thought to range in age from early Coniacian to early Santonian. The age of the plant-bearing sediments in the Asamigawa Member is probably early Coniacian (ca. 89 million years before present; Gradstein *et al.*, 1995), whereas the age of the plant-bearing sediments in the Tamayama Formation is probably early Santonian (ca. 85 million years before present; Gradstein *et al.*, 1995).

Bulk samples of ca. 500 kg of carbonaceous, black, poorly sorted sandy siltstone were dried in the laboratory, disaggregated in water and sieved through a 0.3 mm mesh. Recovered carbonaceous debris was then cleaned in hydrofluoric and hydrochloric acids, thoroughly rinsed in water, and dried in air. Individual specimens selected for scanning electron microscopy were mounted on scanning electron microscope stubs, sputter coated with platinum-palladium and examined in a Hitachi S-800 field emission scanning electron microscope. All specimens are deposited in the paleobotanical collections of the Field Museum of Natural History, Chicago (PP).

Systematic description

Class Magnoliopsida (angiosperms)

Genus *Esgueiria* Friis, Pedersen and Crane, 1992

The genus was established by Friis, Pedersen and Crane (1992) based on material from two localities of Campanian–Maastrichtian age in the northern part of the Western Portuguese Basin, Beira Litoral, Portugal. Two species were distinguished: *Esgueiria adenocarpa* from the Esgueira locality (the type species), and *Esgueiria miraensis* from the Mira locality.

Esgueiria futabensis sp. nov.

Figures 1–11–1–8, 2–1, 2–2, 2–4, 2–5

Material.—PP45389 (holotype). Other specimens; PP45390–PP45417.

Type Locality and Horizon.—Kamikitaba plant mesofossil assemblage (sample F16), along a tributary of the Kitaba River in Kamikitaba, Hirono-machi, (Study Route B of Ando *et al.* 1995; 37°12'N, 140°57'E).

Etymology.—Named after the Futaba Group, the geological unit from which the specimens were recovered.

Specific Diagnosis.—Ovary and fruit narrowly elongate, rounded at the base. Peltate (glandular) trichomes on the base of the styles, and also in rows, often of ten or more, on the hypanthium. Simple trichomes densely spaced on the surface of the ovary, calyx and styles. Prominent receptacular mounds present between the stamens and the perianth.

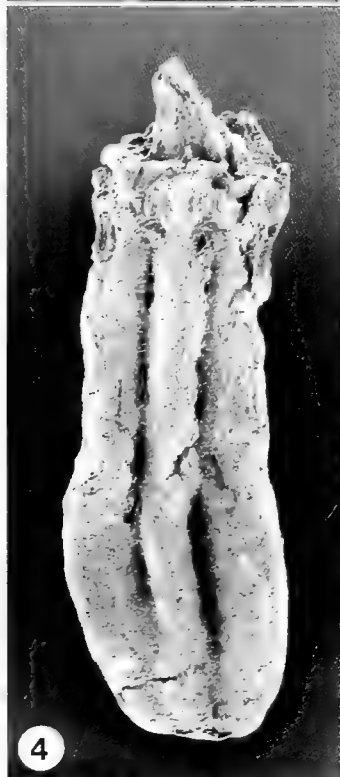
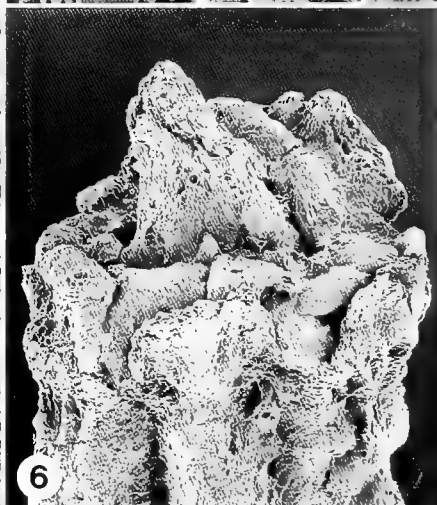
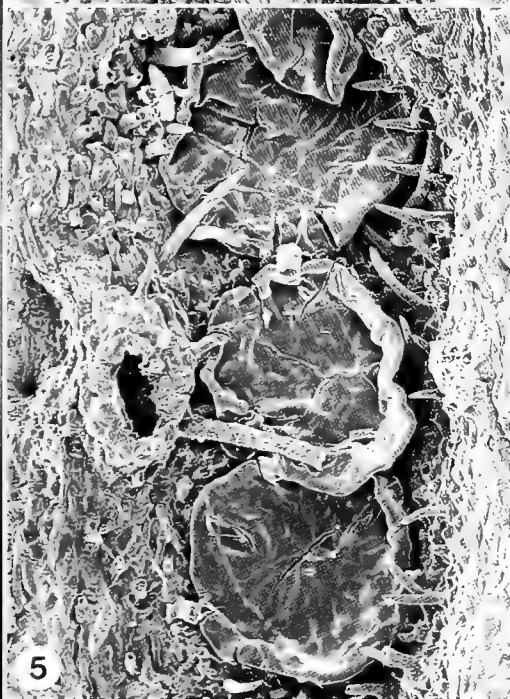
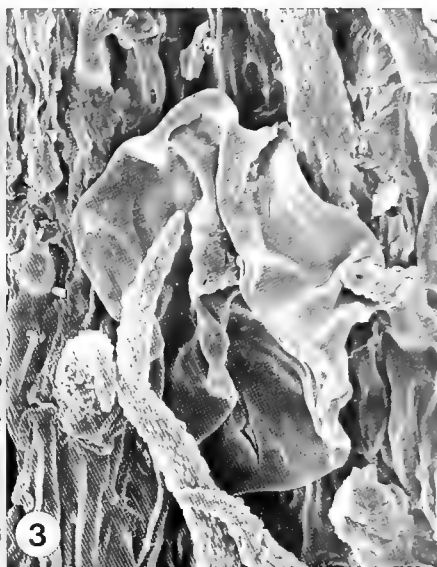
Dimensions.—All specimens lacking a well-preserved corolla: length of ovary: (1.85–) 2.76 (–3.3) mm; breadth of ovary: (0.7–) 1.12 (–1.5) mm; length of sepals: unknown; breadth of sepals: (0.3–) 3.62 (–0.4) mm; 25 specimens measured. Pollen not identified.

Description and Remarks.—The species is known from 29 complete or fragmentary flowers from the Kamikitaba assemblage preserved mainly as charcoallified specimens. Similar material from the Kohisa assemblage is not referred to *E. futabensis*, and probably represents a different species of *Esgueiria* (see below). Many of the specimens are broken or abraded fragments of the inferior ovary, but almost all show either the distinctive peltate glands, or the remains of the glands and their secretion in one or more longitudinal grooves in the ovary wall. None of the specimens is a bud and most of the material probably represents mature fruits with a partially persistent perianth and androecium. None of the specimens has yielded information on inflorescence structure, anthers, pollen or ovules.

Flower: Flowers are epigynous (Figure 1–1) and the calyx is visible in most specimens. Remains of filament and styles bases are also commonly preserved. Unequivocal remains of the petals are rarely present. None of the specimens have a pedicel or prophyll preserved.

Perianth: The calyx consists of five free sepals (Figure 1–2). In all specimens the calyx lobes are broken and their shape cannot be established reliably (Figures 1–2, 1–6, 2–5).

→ **Figure 1.** *Esgueiria futabensis* sp. nov., Kamikitaba assemblage, Asamigawa Member, Ashizawa Formation (lower Coniacian), Futaba Group, Fukushima Prefecture, northeastern Honshu, Japan. **1.** Holotype, lateral view of well-preserved epigynous flower showing peltate and simple trichomes on the ovary wall, note remains of sepals and three styles at flower apex, as well as the protruding hemispherical glands in the outer tissues of the ovary wall, PP45389, $\times 35$. **2.** Holotype, apex of flower showing sepals, possible remains of corolla, receptacular mounds, stamen filaments and three styles, PP45389, $\times 73$. **3.** Holotype, detail of small, peltate, trichome from base of style, note also thick wall of broken trichome, PP45389, $\times 930$. **4.** Lateral view of abraded specimen showing ovary with longitudinal ribs denuded of trichomes, note remains of sepals and stout style base at the apex of the flower, PP45403, $\times 35$. **5.** Holotype, detail of peltate and simple trichomes from ovary wall, note also the opening of a hemispherical gland in the ovary wall, PP45389, $\times 100$. **6.** Detail of apical portion of specimen in Figure 1–4 showing sepals, receptacular mounds, filament bases and stout base of style, PP45403, $\times 72$. **7.** Holotype, detail of simple trichome from ovary wall, note verrucate surface, PP45389, $\times 920$. **8.** Detail of apex of flower in Figure 1–4 showing remains of sepals, ten prominent receptacular mounds, eight (possibly nine) filament bases and stout base of style, PP45403, $\times 72$.



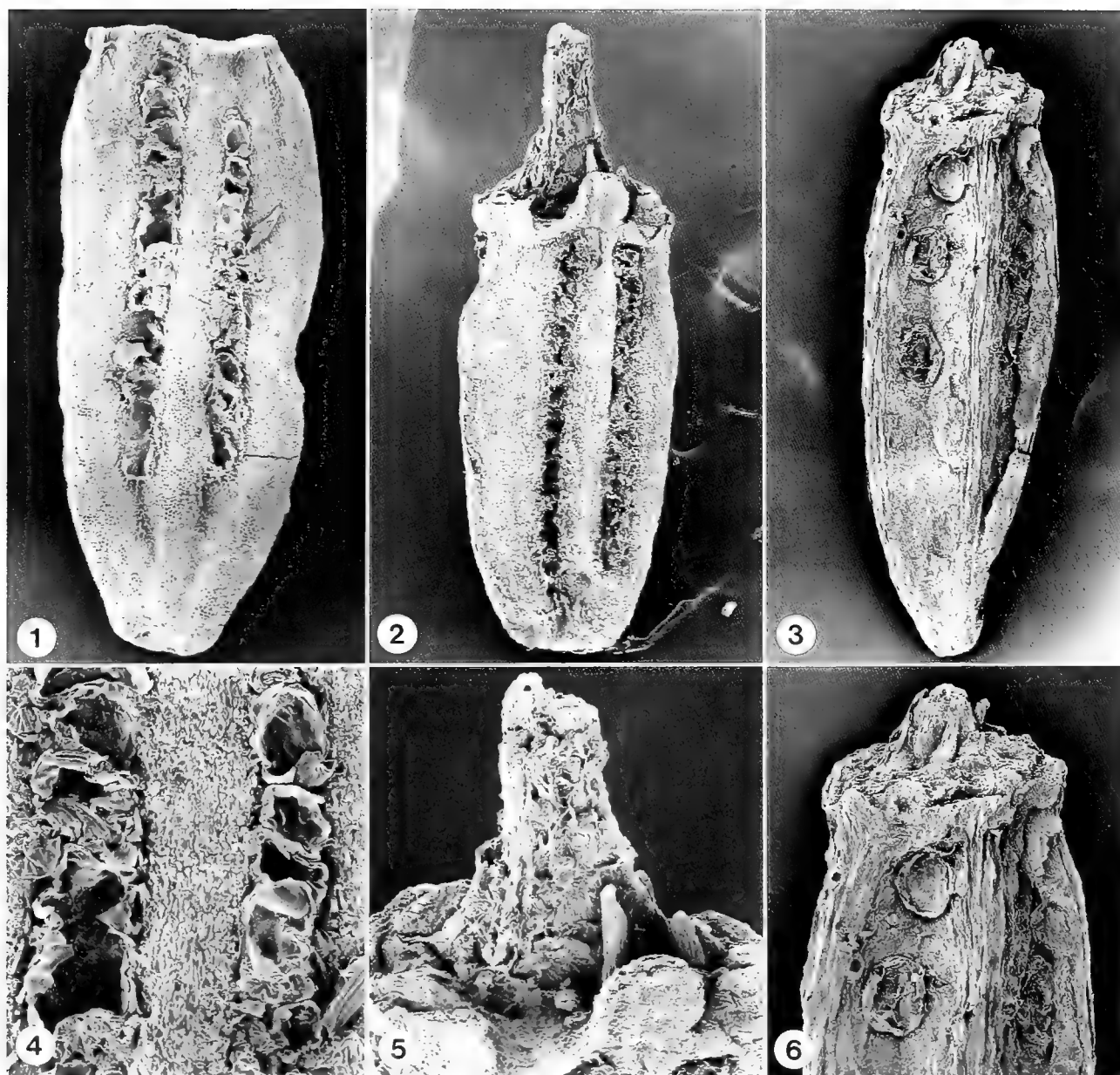


Figure 2. *Esgueiria futabensis* sp. nov. and *Esgueiria* sp., Futaba Group, Fukushima Prefecture, northeastern Honshu, Japan. 1, 2, 4, 5, *Esgueiria futabensis* sp. nov., Kamikitaba assemblage, Asamigawa Member, Ashizawa Formation (lower Coniacian). 3, 6, *Esgueiria* sp., Kohisa assemblage, middle part of the Tamayama Formation (lower Santonian). 1. Lateral view of abraded specimen showing numerous peltate trichomes in two grooves in the ovary wall, PP45391, $\times 32$. 2. Lateral view of abraded specimen showing remains of peltate trichomes in two grooves in the ovary wall, note remains of sepals and stout base of style at the floral apex, PP45393, $\times 30$. 3. Lateral view of compressed specimen showing three prominent peltate trichomes on the ovary wall, note that the peltate trichomes are larger and fewer than in *E. futabensis*, PP45419, $\times 17$. 4. Detail of specimen in Figure 2-1 showing remains of peltate trichomes and unabraded portion of ovary wall, PP45391, $\times 90$. 5. Apex of specimen in Figure 2-2 showing sepals, bases of two filaments and stout base of style, PP45393, $\times 67$. 6. Apex of specimen in Figure 2-3 showing stamen filament surrounding stout base of style, note remains of receptacular mounds between the sepals and stamen bases, PP45419, $\times 27$.

However, there are sufficient specimens in which parts of the calyx are preserved to infer that it was persistent through fruit development. The corolla is not clearly visible in any of the specimens, although a few show fragments of tissue that may represent the bases of petals. The rare presence of the corolla in more than 1,000 specimens of *E. adenocarpa* led to the conclusion that the corolla was probably caducous (Friis *et al.*, 1992), and this may also have been the case in *E. futabensis*.

Receptacular mounds: Most specimens show prominent, more or less ellipsoidal mounds of tissue, ca. 0.2 mm broad and ca. 0.1 mm deep, on the receptacle between the filament bases and the calyx (Figures 1-6, 1-8). In one specimen there are ten mounds that alternate with the stamen bases (Figure 1-8). The nature of these mounds is uncertain, but judging from their position and swollen structure (Figures 1-2, 1-6) it is possible that they are nectary lobes. A possible nectary was observed in *E. adenocarpa*, but in the more usual position for a disc nectary, between the stamens and the style bases (Friis *et al.*, 1992). In *E. futabensis* it is clear that the receptacular mounds are outside the androecium between the sepals and the stamens (Figure 1-8).

Androecium: None of the specimens has a complete stamen preserved and we have been unable to detect pollen on any of the flowers. However, the position of the stamen filaments indicates stamens were both opposite to, and alternate with, the sepals (Figure 1-8). Based on this pattern an androecium of ten stamens would be inferred. However, the best preserved androecium (Figure 1-8) shows the remains of only eight (or possibly nine) filaments. It is uncertain whether this indicates incomplete preservation, or whether less than ten stamens developed as in *E. adenocarpa* (Friis *et al.*, 1992). There is no clear indication that stamens were arranged in more than one whorl (Figure 1-8).

Gynoecium: The ovary is inferior and unilocular. The holotype clearly shows that there were three free styles, at least distally (Figure 1-2). Proximally, however the styles appear to have been fused into a single, stout, style base (Figures 1-6, 2-5). The ovary is narrowly elongated, more or less parallel-sided and with a rounded base (Figures 1-1, 1-4, 2-1, 2-2). The ovary wall is pleated into five longitudinal grooves that alternate with sepals, and five longitudinal ridges that are on the same radius as the sepals. The ovary wall is about 0.05 mm thick. In several specimens there are protruding hemispherical glands, ca. 0.1 mm in diameter, in the outer tissues of the ovary wall. In abraded specimens that lack the epidermis the inner layers of the ovary wall are seen to be composed of small equiaxial sclerenchyma cells ca. 0.01 mm in diameter. Lining the locule there is a inner epidermis of larger cuboidal cells.

Trichomes: Two different types of trichomes have been observed on the specimens. They are best developed and most easily observed on the surface of the ovary but also occur on the stout style base.

Simple trichomes: Simple hairs are scattered all over the ovary and other floral organs. The hairs may be up to ca. 0.2 mm long, are more or less parallel-sided for much of their length, and appear to be unicellular (Figure 1-7). At the apex they have an acute point. Broken specimens show

that the trichomes are thick-walled (Figure 1-3). The trichome wall close to the point of attachment seems to be thinner and somewhat collapsed (Figure 1-7). In well-preserved specimens the trichome wall is ornamented with distinctive elongated verrucae (Figures 1-3, 1-7).

Peltate trichomes: Peltate trichomes (inferred to have been glandular) are arranged in a single row in the grooves in the ovary wall (Figures 1-5, 2-4). The peltate trichomes never occur side-by-side. Smaller peltate trichomes also occur on the style bases (Figure 1-3). On the ovary wall the peltate trichomes are typically more or less circular, 0.12–0.18 mm in diameter, and appear to consist of a central stalk and a shieldlike head. A clear radiating structure among the cells comprising the head has not been seen. The number of peltate trichomes in a single row varies, but it is often between 10 and 20 (Figure 1-1, 2-1). Frequently, under the light microscope, the peltate trichomes appear to be embedded in a black shiny substance, which is often present even when the trichomes themselves are not clearly visible (Figure 2-2). We infer that this represents the remains of a secretion associated with the glandular trichomes. Peltate trichomes also occur on the style-bases of well-preserved specimens scattered among the simple hairs. These trichomes are generally smaller (ca. 0.06 mm in diameter) and less prominent than those on the ovary wall but are similar in structure (Figure 1-3).

Comparison

Esgueiria futabensis clearly shows the diagnostic features of the genus (Friis *et al.*, 1992). The flowers are small, epigynous and bisexual with the perianth and androecium organized on a basically pentamerous plan. There is a calyx of five free sepals and an androecium with more than five stamens. The ovary is unilocular with three styles. The indumentum consists of simple stiff hairs and the characteristic multicellular, peltate trichomes.

Esgueiria futabensis is clearly distinguished from the two other species of the genus. It differs from the type species, *E. adenocarpa*, in being generally larger: (1.85–) 2.76 (–3.3) mm rather than (1.5–) 1.88 (2.2) mm long. The shape of the ovary is also more or less parallel-sided, rather than obovate, and the base of the ovary is rounded rather than pointed (compare Figures 1-1, 1-4, 2-1, 2-2 with Friis, Pedersen and Crane, 1992, Plate 1). The peltate trichomes are smaller (0.12–0.18 mm in diameter) in *E. futabensis* than in *E. adenocarpa* (0.2–0.3 mm in diameter). Also significant is the number of peltate glands in a single groove on the ovary wall, which is often 10–20 in *E. futabensis*, compared with a maximum of five or six in *E. adenocarpa*.

The occurrence of peltate glands on the style bases (Figure 1-3) is a further difference between *E. futabensis* and *E. adenocarpa*, but a similarity with *E. miraensis*. However, compared to *E. miraensis*, *E. futabensis* is larger: length of ovary (1.85–) 2.76 (–3.3) mm compared to 0.8–0.95 mm. The ovary of *E. futabensis* is also long and narrow, rather than campanulate as in *E. miraensis*.

Other *Esgueiria* flowers are known from the Kohisa plant mesofossil assemblage, which is younger (early Santonian)

than the Kamikitaba assemblage that yielded *E. futabensis*. However, the Kohisa specimens are larger than those from Kamikitaba (length of ovary [2.75–] 3.5 [–4] mm), are more obovate in shape with a more pointed base, and also have significantly larger peltate trichomes (Figures 2–3, 2–6). These specimens may represent a fourth species of *Esgueiria*, but because only eight specimens are known (PP45418–PP45425), they are here left unassigned as *Esgueiria* sp.

Discussion

In terms of systematic affinities, *E. futabensis* does not add to previous discussions of a relationship between *Esgueiria* and the extant angiosperm family Combretaceae. However, this new species is important in several respects. It documents the occurrence of mesofossil assemblages with well-preserved angiosperm flowers in the Upper Cretaceous of Japan that are comparable in their quality of preservation to those recently described from eastern North America, Europe and central Asia. It adds a new species to the very small number of fossil angiosperm reproductive structures so far described from the Upper Cretaceous of Japan (Stopes and Fujii, 1910; Ohana and Kimura, 1987; Nishida, 1985, 1991, 1994; Nishida and Nishida 1988; Nishida *et al.*, 1996). It also provides the first evidence of botanically informative plant fossil assemblages (other than palynofloras; Miki, 1977; Takahashi, 1988) in the Futaba Group.

The discovery of *Esgueiria futabensis* also has interesting biogeographic implications and extends substantially the range of a genus previously known only from the Campanian-Maastrichtian of Portugal. Based on pollen and spore assemblages Portugal was part of the Normapolles Province during the Late Cretaceous. Japan is generally included in the *Aquilapollenites* Province (Herngreen *et al.*, 1996) based on the first appearance of triporate grains in Late Cretaceous sediments younger than those of the Futaba Group (Miki, 1977). The occurrence of *Esgueiria* in both eastern Asia and southern Europe documents that some Late Cretaceous floristic elements had very broad geographic distributions, presaging the strong floristic similarities evident at middle and high latitudes of the Northern Hemisphere during the early Tertiary.

Acknowledgments

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Boreal-type brachiopod *Yakovlevia* from the Middle Permian of Japan

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Abstract. The following three species of the Boreal-type brachiopod genus *Yakovlevia* are described from the Middle Permian (Kungurian to Ufimian) of the Hida Gaian (=Hida Marginal) and South Kitakami Belts, Japan: *Y. kaluzinensis* Fredericks, *Y. mammata* (Keyserling) and *Y. mammatiformis* (Fredericks). The occurrence of *Yakovlevia* together with various Boreal and Tethyan-type brachiopods in the Middle Permian of the two belts suggests that these regions were probably a continental shelf at the eastern margin of the Sino-Korean block in Middle Permian time.

Key words: Boreal-type brachiopod, Hida Gaian Belt, Middle Permian, Sino-Korean block, South Kitakami Belt, *Yakovlevia*

Introduction

Brachiopods are important and useful for Permian global palaeobiogeography as the predominant element in the benthic fauna at that time (Stehli, 1973; Waterhouse and Bonham-Carter, 1975; Grunt, 1995; Shi *et al.*, 1995; Jin and Shang, 1997). *Yakovlevia* is a typical Boreal-type, Middle Carboniferous to Middle Permian productoid genus belonging to the family Yakovleviidae Waterhouse, 1975. This genus was established by Fredericks in 1925, with *Chonetes* (*Yakovlevia*) *kaluzinensis* Fredericks, 1925 from the Middle Permian Chandalaz Formation of Cape Kalouzin in the Vladivostok area, South Primorye as the type species. The morphology and classification of *Yakovlevia* and related genera have been fully discussed by Licharew (1947), Muir-Wood and Cooper (1960), Kotljar (1961), Muir-Wood (1965), Cooper and Grant (1975), Waterhouse (1975), and Shi (1995). Concerning the relationship of *Yakovlevia* with *Muirwoodia* Licharew, 1947, I follow Kotljar (1961), Cooper and Grant (1975), and Shi (1995), all of whom considered *Muirwoodia* as a junior synonym of *Yakovlevia*.

The purpose of this paper is to describe three *Yakovlevia* species, *Y. kaluzinensis* Fredericks, 1925, *Y. mammata* (Keyserling, 1846), and *Y. mammatiformis* (Fredericks, 1926), from the Middle Permian (Kungurian to Ufimian) of the Hida Gaian and South Kitakami Belts, Japan, discussing their palaeobiogeographical significance. The material utilized is: eight specimens of *Y. kaluzinensis* from the lower part of the Moribu Formation in the Moribu area, Hida Mountains (Hida Gaian Belt), central Japan; two specimens of *Y. mammata* from the lower Kanokura Formation in the Kesen-numa area, southern Kitakami Mountains (South Kitakami Belt), northeast Japan; and the single specimen of *Y.*

mammatiformis from the upper Irishikura Formation in the Takakurayama area, Abukuma Mountains (South Kitakami Belt), northeast Japan (Figure 1). These specimens are housed in the Department of Geology, Faculty of Science, Niigata University, Niigata (NU-B) and the Institute of Geology and Palaeontology, Tohoku University, Sendai (IGPS).

Palaeobiogeographical significance of *Yakovlevia*

Recently Shi (1995) summarized the stratigraphical and geographical distribution of *Yakovlevia* using 45 species of this genus. According to him, the genus is distributed from the Middle Carboniferous to Middle Permian of the Boreal Realm and the transitional zone between the Boreal and Tethyan Realms, namely, the Northern Transitional Zone (Sino-Mongolian Province) and the Cordilleran Province (see Shi, 1995, figs. 2, 3, table 1). The former transitional zone is almost equal to the Inner Mongolian-Japanese Transition Zone of Tazawa (1991).

As shown in Figure 2, the three *Yakovlevia* species described below clearly indicate a Boreal distribution. *Y. kaluzinensis* has been known from the Middle Permian (Kungurian to Ufimian) of South Primorye, eastern Russia, and the Hida Mountains, central Japan (Fredericks, 1925; Muir-Wood and Cooper, 1960; Kotljar, 1961; Licharew and Kotljar, 1978; Horikoshi *et al.*, 1987; Tazawa, 1987). *Y. mammata* has been known from the Lower Permian (Artinskian) to Middle Permian (Guadalupian) of Spitsbergen; Timan and Pechora, northern Russia; Upper Yukon River, Yukon Territory; Grinnell Peninsula, Devon Island, Arctic Canada; Tien Shan, West China; Ekenalsileng, Jisu (Zhesi), Dong Ujimqin, Xi Ujimqin and Horqin Youyi Qianqi, Inner Mongolia, North China; South Primorye, eastern Russia;



Figure 1. Map showing the fossil localities.

southern Kitakami Mountains, northeast Japan (Keyserling, 1846; Koninck, 1847; Tschernyschew, 1902; Keidel, 1906; Chao, 1927; Grabau, 1931; Stepanov, 1937; Muir-Wood and Cooper, 1960; Harker in Harker and Thorsteinsson, 1960; Kotljar, 1961; Gobbett, 1963; Brabb and Grant, 1971; Ifanova, 1972; Lee and Gu, 1976; Licharew and Kotljar, 1978; Lee and Gu in Lee *et al.*, 1980; Liu and Waterhouse, 1985; Tazawa, 1987; Malkowski, 1988; Zhang, 1990; Nakamura *et al.*, 1992; Kalashnikov, 1993). *Y. mammatiformis* is distributed in the Lower Permian (Sakmarian) to Middle Permian (Kungurian) of the northern Urals, Timan, Pechora Basin and Novaya Zemlya, northern Russia; Omolon Massif, northeastern Russia; South Primorye, eastern Russia; Abukuma Mountains, northeast Japan (Fredericks, 1926; Kotljar, 1961; Mironova, 1964; Yanagisawa, 1967; Zavadowsky and Stepanov in Zavadowsky *et al.*, 1970; Ifanova, 1972; Kulikov, 1974; Kalashnikov, 1983, 1993).

The Middle Permian brachiopod faunas of the Hida Gaien and South Kitakami Belts are characterized by a mixture of Boreal and Tethyan elements, e.g., *Yakovlevia*, *Cancrinella*, *Waagenoconcha*, *Megousia*, *Stenosisma*, and *Spiriferella* as the Boreal-type genera, and *Leptodus*, *Enteletes*, *Transenatia*, *Permudaria*, and *Urushtenoidea* as Tethyan-type genera (Tazawa, 1987, 1991, 1992; Nakamura and Tazawa,

1990), and closely resemble those of South Primorye, North-east China and Inner Mongolia (Tazawa, 1987, 1991, 1992). The occurrence of *Yakovlevia* together with various Boreal- and Tethyan-type brachiopods in the Middle Permian of the Hida Gaien and South Kitakami Belts supports the opinion of Tazawa (1991, 1992), who considered that 1) the above regions belonged to the Southern Subzone of the Inner Mongolian-Japanese Transition Zone, and that 2) this subzone was being probably a piece of continental shelf bordering the eastern margin of the Sino-Korean block, which was situated at a middle northern palaeolatitude in Middle Permian time (Figure 2).

Systematic descriptions

Order Productida Waagen, 1883
 Suborder Productidina Waagen, 1883
 Superfamily Linoproductoidea Stehli, 1954
 Family Yakovleviidae Waterhouse, 1975
 Genus ***Yakovlevia*** Fredericks, 1925

Type species.—*Chonetes* (*Yakovlevia*) *kaluzinensis* Fredericks, 1925.

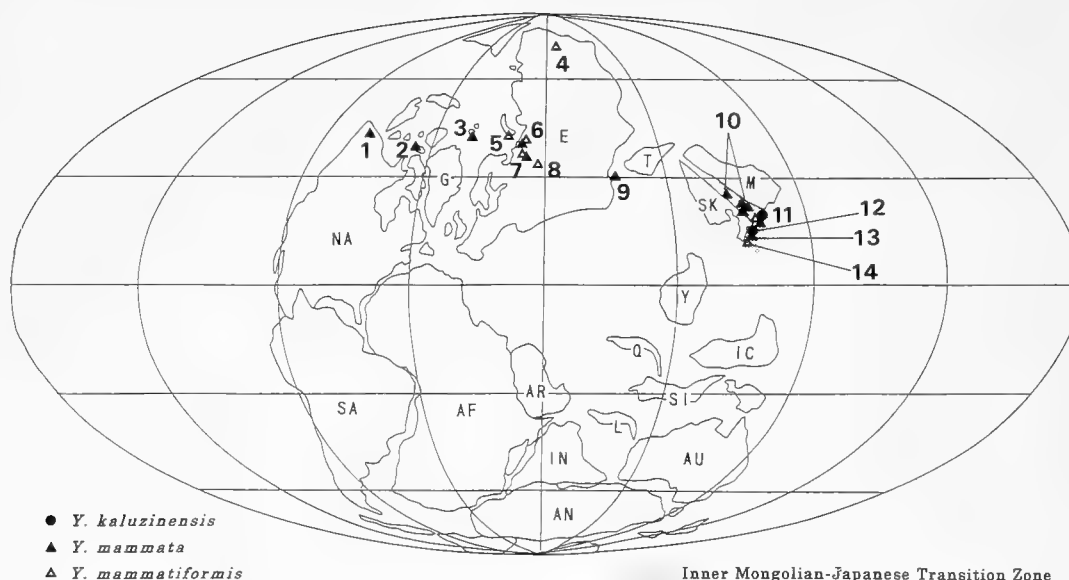


Figure 2. Geographical distribution of *Yakovlevia kaluzinensis* Fredericks, *Yakovlevia mammata* (Keyserling) and *Yakovlevia mammatiformis* (Fredericks) in Middle Permian. (Palaeogeographic map after Ziegler *et al.*, 1996). 1. Yukon Territory, 2. Devon Island, 3. Spitsbergen, 4. Omolon Massif, 5. Novaya Zemlya, 6. Pechora Basin, 7. Timan, 8. northern Urals, 9. Tien Shan, 10. Inner Mongolia, 11. South Primorye, 12. Moribu, Hida Mountains, 13. Kesennuma, southern Kitakami Mountains, 14. Takakurayama, Abukuma Mountains. AF: Africa, AN: Antarctica, AR: Arabia, AU: Australia, E: Eurasia, G: Greenland, IC: Indochina, IN: India, L: Lhasa, M: Mongolia, NA: North America, Q: Qangtang, SA: South America, SI: Sibumasu, SK: Sino-Korea, T: Tarim, Y: Yangtze.

Yakovlevia kaluzinensis Fredericks, 1925

Figures 3–7—15

Chonetes (*Yakovlevia*) *kaluzinensis* Fredericks, 1925, p. 7, pl. 2, figs. 64–66.

Yakovlevia kaluzinensis Fredericks. Muir-Wood and Cooper, 1960, pl. 133, figs. 5, 6; Kotljar, 1961, text-figs. 1–3; Licharew and Kotljar, 1978, pl. 14, figs. 1, 2.

Yakovlevia sp. Horikoshi *et al.*, 1987, text-figs. 3A, B; Tazawa, 1987, text-fig. 1.7.

Material.—Eight specimens, from the lower Moribu Formation in the Moribu area, Hida Mountains (Hida Gaiken Belt), central Japan: (1) external and internal moulds of a pedicle valve, NU-B157; (2) internal moulds of three pedicle valves, NU-B158–160; (3) external and internal moulds of two brachial valves, NU-B161, 162; (4) external moulds of two brachial valves, NU-B163, 164.

Description.—Shell large for genus, transversely subrectangular in outline, with greatest width at hinge line; length about 37 mm, width about 44 mm in the smaller pedicle valve specimen (NU-B157); length 38 mm, width about 60 mm in the largest and best preserved brachial valve specimen (NU-B163).

Pedicle valve gently convex on venter, strongly geniculated, and followed by a long trail. Umbo small. Ears large, prominent, but not clearly differentiated from visceral part. Sulcus narrow and shallow, originating near umbo, and extending to anterior margin. External ornament of pedicle

valve invisible except for a row of oblique spines just anterior to the posterior margin. Brachial valve nearly flat on visceral disc, strongly geniculated, and followed by a short trail. Fold narrow and low on anterior half of valve. External surface of brachial valve ornamented by numerous fine costellae and several weak, irregular concentric rugae on visceral disc, costellae only on trail; costellae often bifurcating and intercalating, numbering 11–13 costellae in 5 mm at midvalve.

Pedicle valve interior with a pair of small, elongate subtrigonal adductor scars and two large diductor scars. Diductor scars striated anteriorly and encircled by a strong ridge posterolaterally. Internal structure of brachial valve obscure in the present material.

Comparison.—The Moribu specimens are referred to *Yakovlevia kaluzinensis* Fredericks, 1925, originally described by Fredericks (1925) from the Middle Permian in size and shape of the shells, especially in the transversely subrectangular outline.

Yakovlevia impressa (Toula, 1875, p. 236, pl. 5, figs. 1a–c) from the Middle Permian of Spitsbergen differs from *Y. kaluzinensis* in having larger and more prominent ears.

Yakovlevia mammata (Keyserling, 1846)

Figures 3–1—5

Productus mammatus Keyserling, 1846, p. 206, pl. 4, figs. 5–5b; Koninck, 1847, p. 49, pl. 7, figs. 4a–e; Tschernyschew, 1902, p. 295, pl. 35, figs. 4–6; Keidel, 1906, p. 367, pl. 12, figs. 5a,

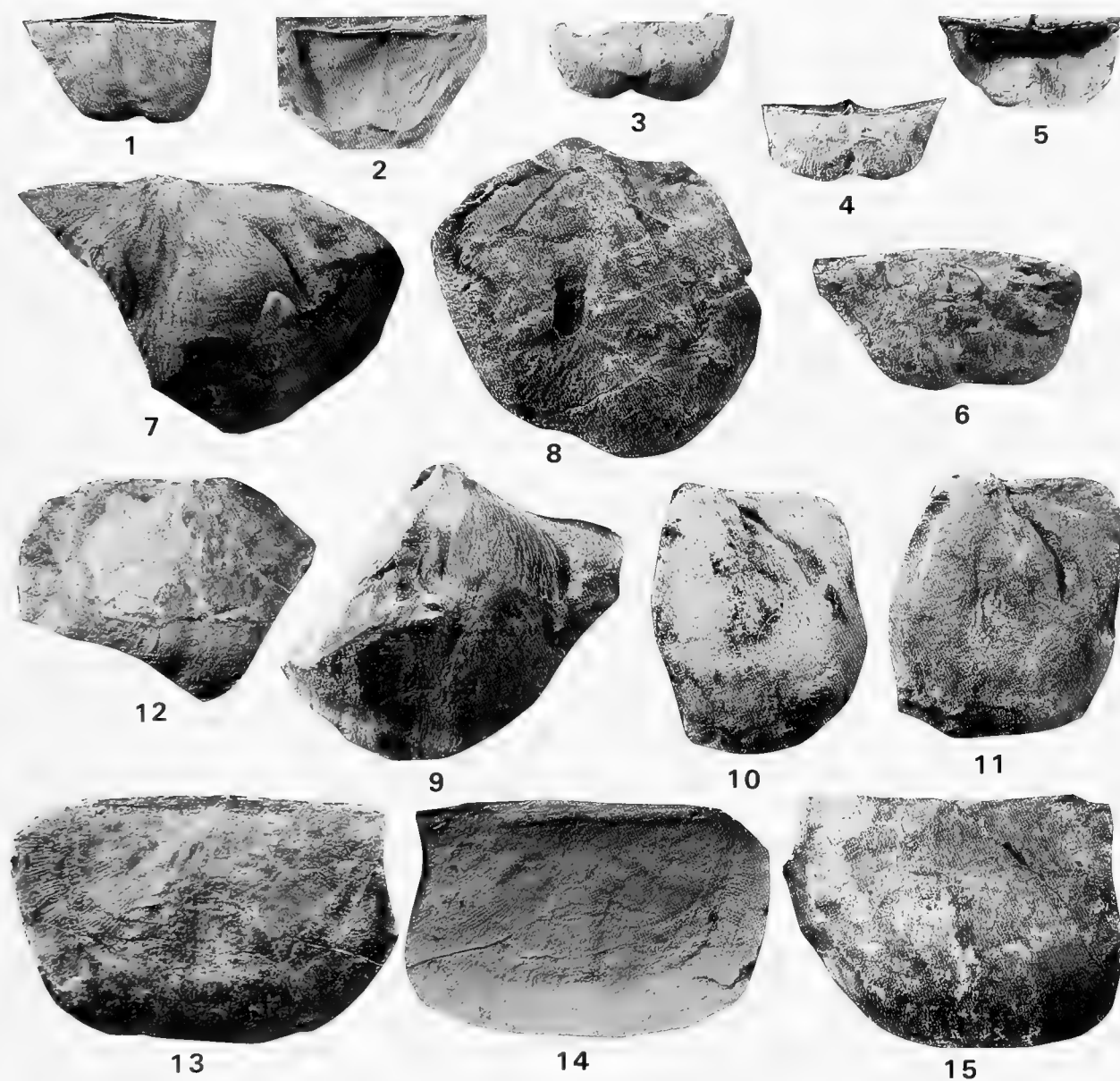


Figure 3. 1–5. *Yakovlevia mammata* (Keyserling). 1, 2. External mould of a brachial valve and the latex cast, NU-B166. 3–5. latex cast of a pedicle valve exterior, external mould of a brachial valve and the latex cast, NU-B165. 6. *Yakovlevia mammatiformis* (Fredericks), external mould of a brachial valve, IGPS coll. cat. no. 86649. 7–15. *Yakovlevia kaluzinensis* Fredericks. 7–9. internal moulds of pedicle valve specimens, 7. NU-B158, 8. NU-B160, 9. NU-B159. 10, 11. external mould of a pedicle valve and the latex cast, NU-B157; 12. external mould of a brachial valve, NU-B162; 13, 14. external mould of a brachial valve and the latex cast, NU-B163. 15. external mould of a brachial valve, NU-B161. (All figures in natural size)

b.
Linoproductus ? *mammatus* (Keyserling). Chao, 1927, p. 146, pl. 15, figs. 10–14.
Productus (*Linoproductus* ?) *mammatus* Keyserling. Grabau, 1931, p. 288, pl. 29, figs. 10–14.
Productus (*Thomasina*) *mammatus* Keyserling. Stepanov, 1937, p. 127, 177, pl. 2, figs. 5–7.

Muirwoodia mammata (Keyserling). Muir-Wood and Cooper, 1960, pl. 120, figs. 9–11; Harker in Harker and Thorsteinsson, 1960, p. 58, pl. 16, figs. 1–5; Gobbett, 1963, p. 112, pl. 13, figs. 23–28; Lee and Gu, 1976, p. 263, pl. 159, figs. 7–9; pl. 163, figs. 2a, b; pl. 164, figs. 3–4; pl. 170, figs. 6, 7; Licharew and Kotljars, 1978, pl. 14, figs. 3–5; Liu and Waterhouse, 1985, p. 17, pl. 4, figs. 4–6; Nakamura *et al.*, 1992, pl. 1, figs. 4a, b;

Kalashnikov, 1993, p. 63, pl. 19, figs. 1-3.

Yakovlevia mammatus Keyserling. Kotljar, 1961, text-figs. 4-6.

Yakovlevia mammata (Keyserling). Brabb and Grant, 1971, p. 16, pl. 1, figs. 9-12, 33-36; Ifanova, 1972, p. 121, pl. 7, figs. 4-5; Malkowski, 1988, p. 40, pl. 5, fig. 6; Zhang, 1990, pl. 2, figs. 4, 7, 9.

Yakovlevia paragreenlandica Lee and Gu in Lee *et al.*, 1980, p. 382, pl. 171, figs. 5-7.

Muirwoodia sp. Tazawa, 1987, text-fig. 1.6.

Material.—Two specimens, from the lower Kanokura Formation of Kamiyasse and Omotematsukawa in the Kesen-numa area, southern Kitakami Mountains (South Kitakami Belt), northeast Japan: (1) external and internal moulds of a pedicle valve, NU-B165; (2) an external mould of a brachial valve, NU-B166.

Description.—Shell small for genus, transversely subtrapezoidal in outline, with greatest width at hinge line; length 13 mm+, width 28 mm in the pedicle valve specimen (NU-B165); length 16 mm, width 29 mm in the brachial valve specimen (NU-B166).

Pedicle valve moderately and unevenly convex in lateral profile, slightly convex on venter, strongly geniculated, and followed by a short trail. Cardinal extremities acute. Ears large, not clearly demarcated from visceral part. Sulcus narrow and shallow on venter, becoming wide and deep on trail. Brachial valve nearly flat on visceral disc, strongly geniculated, and followed by a short trail. Fold originating at about midvalve, narrow and low on visceral disc, but wide and distinct on trail. External surfaces of both valves ornamented by numerous fine capillae and several weak, irregular, concentric rugae on visceral disc, capillae only on trail; capillae often bifurcated and intercalated, numbering 14-15 capillae in 5 mm at midvalve.

Pedicle valve interior with large, flabellate diductor scars, occupying posterior half of valve, deeply depressed and bounded by marginal ridges posterolaterally. Other internal structures not observed.

Comparison.—The specimen numbered NU-B166, from the lower Kanokura Formation of the southern Kitakami Mountains, was first figured by Tazawa (1987, text-fig. 1.6) as *Muirwoodia* sp., but is now referred to *Yakovlevia mammata* (Keyserling, 1846), originally described by Keyserling in 1846 from the Lower Permian (possibly Sakmarian) of the Pechora Land, northern Russia, on the basis of similarities in size, outline and external ornament.

Yakovlevia paragreenlandica Lee and Gu (in Lee *et al.*, 1980), from the Middle Permian Dashizhai Formation of Horqin Youyi Qianqi, eastern Inner Mongolia may be conspecific with the present species.

The shells described and figured by Grabau (1936, p. 107, pl. 6, figs. 5-6; pl. 11, figs. 4-6) as *Productus mammatus* Keyserling from the Maping Limestone in the Guangxi and Guizhou Provinces, South China differ from *Y. mammata* in having smaller ears and coarser costellae.

Both species, *Yakovlevia artiensis* (Tschernyschew, 1889, p. 279, pl. 7, figs. 29-31) from the Artinskian of the Central Urals and *Yakovlevia greenlandica* (Dunbar, 1955, p. 103, pl. 16, figs. 1-17) from the Middle Permian (Guadalupian) of Central East Greenland are distinguished from the present

species by their fewer and coarser costellae.

Yakovlevia mammatiformis (Fredericks, 1926)

Figure 3-6

Productus mammatiformis Fredericks, 1926, p. 87, pl. 3, figs. 4-6.
Yakovlevia mammatiformis Fredericks. Kotljar, 1961, text-figs. 7, 8.

Yakovlevia mammatiformis (Fredericks). Mironova, 1964, p. 97, pl., figs. 14a-v; Zavodowsky and Stepanov in Zavodowsky *et al.*, 1970, p. 114, pl. 35, figs. 8-10; Ifanova, 1972, p. 119, pl. 6, figs. 15-16; pl. 7, figs. 1-2; Kalashnikov, 1983, p. 210, pl. 49, figs. 5, 6, 9; Kalashnikov, 1993, p. 61, pl. 16, figs. 1-4.

Linoproductus cf. mammatus (Keyserling). Yanagisawa, 1967, p. 88, pl. 2, fig. 7.

Muirwoodia mammatiformis (Fredericks). Kulikov, 1974, p. 89, pl. 3, figs. 6a-v.

Material.—One specimen, an external mould of a brachial valve, IGPS coll. cat. no. 86649, from the upper Irishikura Formation in the Takakurayama area, Abukuma Mountains (South Kitakami Belt), northeast Japan.

Description.—Shell medium for genus, transverse, subtrapezoidal in outline, with greatest width at hinge line; length 22 mm, width 42 mm in the brachial valve specimen.

Brachial valve gently concave on visceral disc, strongly geniculated at anterior margin of visceral disc, and followed by a short trail. Ears large, flat and prominent, obscurely demarcated from visceral disc. Fold moderately high, originating at about midvalve, and rapidly widening anteriorly. External surface of brachial valve ornamented by numerous fine costellae; costellae rounded, with narrow interspaces, numbering 10-11 costellae in 5 mm at midvalve. No spines or spine bases observed.

Comparison.—The single specimen from the Abukuma Mountains was first described by Yanagisawa (1967, p. 88) as *Linoproductus cf. mammatus* (Keyserling), but this specimen is referred to *Yakovlevia mammatiformis* (Fredericks, 1926) on the basis of its size, shape and surface ornament of the brachial valve.

Yakovlevia mammata (Keyserling, 1846) differs from *Y. mammatiformis* in its smaller and less transverse shell, ornamented by more numerous, fine capillae.

Yakovlevia transversa (Cooper, 1957, p. 39, pl. 5, figs. 1-13) from the Middle Permian of Oregon resembles *Y. mammatiformis* in general appearance, but the former is distinguished from the latter by its smaller dimensions, more developed fold commencing a little below the umbo, and fewer and coarser costellae on the brachial valve.

The shells described as *Y. mammatiformis* from the Middle Permian of Gansu, Northwest China (Ding and Qi in Zhang *et al.*, 1983, p. 292, pl. 99, figs. 9a, b), Inner Mongolia, North China (Lee and Gu, 1976, p. 264, pl. 164, figs. 6, 8; pl. 165, figs. 1, 5) and Heilongjiang, Northeast China (Lee *et al.*, 1980, p. 383, pl. 165, figs. 25a, b; pl. 172, fig. 3) are distinguished from the present species by their much larger size.

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Taxonomy and distribution of *Macoma (Rexithaerus)* (Bivalvia : Tellinidae) in the northwestern Pacific

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Abstract. Fossil and Recent *Macoma (Rexithaerus)* of the northwestern Pacific consist of the following three species: *Macoma (Rexithaerus) hokkaidoensis* sp. nov., *M. (R.) sector* Oyama and *M. (R.) shiratoriensis* (Matsubara). Among them, the first species, which is new, is characterized by an elongate shell shape and a low pallial sinus, and is now living in the sea around Hokkaido, Kunashiri Island, Aniva Bay of Sakhalin, Peter the Great Bay and Ussuri Bay of Primorye. The oldest species, *M. (R.) shiratoriensis* appeared in subtropical waters in the late early Miocene. The Recent and allied species, *M. (R.) sector* and *M. (R.) cf. hokkaidoensis* first occurred in middle Miocene deposits. From the middle Miocene to early Pleistocene, the subgenus was confined to the mild- to cool-temperate realm. In the Holocene, *M. (R.) sector* has extended its range to subtropical waters, while *M. (R.) hokkaidoensis* now inhabits the cool-temperate to subarctic waters.

Key words: Distribution, *Macoma*, *Rexithaerus*, *Macoma (Rexithaerus) hokkaidoensis* sp. nov., taxonomy

Introduction

Rexithaerus Tryon, 1869 is a subgenus of *Macoma* Leach, 1819 and is characterized by a ridge running from beak to posteroventral corner, a bluntly truncated posterior end, a short, rather strong ligamental ridge, and upwardly elevated posterodorsal margin behind ligament.

Two Recent species of the subgenus, *Macoma (Rexithaerus) secta* (Conrad) and *M. (R.) indentata* Carpenter, are known from the northeastern Pacific (Coan, 1971). *Macoma expansa* Carpenter was also included in the subgenus *Rexithaerus* by Coan (1971). However, *M. expansa* Carpenter and a related species, *M. dexioptera* Baxter, 1977 do not belong to the subgenus *Rexithaerus* because they do not have the posterodorsal margin set off as a flange.

On the other hand, only one Recent form in this subgenus, "*M. (R.) sector*" Oyama, has been recorded from around the Japanese Islands, Korea and Far East Russia in the northwestern Pacific (Habe, 1977; Kwon *et al.*, 1993; Kafanov and Lutaenko, 1996).

As a result of our review of the both living and fossil specimens from Japan and adjacent areas, we found a new living species of *Macoma (Rexithaerus)* from southern Hokkaido, Aniva Bay of Sakhalin and Primorye in Far East Russia, and Kunashiri Island.

Macoma (Rexithaerus) originated in northwestern North

America in late Oligocene time and migrated westward into Far East Asia during the late early Miocene (Matsubara, 1994). Recently it has been revealed that many molluscan groups show such a pattern of migration (Amano *et al.*, 1993; Amano and Vermeij, 1998). However, little is known of the details of the process of climatological adaptation in these groups because most of the westward-spreading species have scattered fossil records owing to their rocky shore habitat. As the subgenus *Rexithaerus* lives in muddy bottoms, it is well suited for examining the above biogeographic invasion.

In this paper, we discuss the taxonomy of *Macoma (Rexithaerus)* in the northwestern Pacific in addition to the description of the new species. Based on the temporal and spatial distributions of *Macoma (Rexithaerus)*, we will review the climatological adaptation of this genus after its migration to the Northwest Pacific.

Materials and methods

We have examined specimens of fossil and Recent species stored at Joetsu University of Education (JUE), Museum of Natural History, Tohoku University (IGPS), Sendai, Museum of Nature and Human Activities, Hyogo (MNHAH), Museum of Institute of Marine Biology (MIMB), and Zoological Museum, Far East State University (ZMFU), Vladivostok.

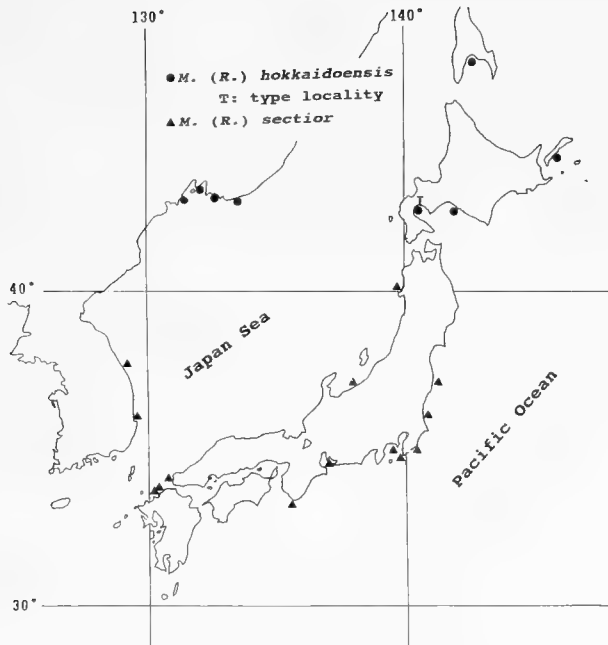


Figure 1. Locality map of the treated or illustrated Recent specimens of *Macoma (Rexithaerus)*.

Concerning the new species, we have examined twenty-one right valves and seventeen left valves from the beach of Oshamanbe and Yufutsu along Funka Bay, Hokkaido, one specimen from the Pleistocene Narita Formation in Chiba Prefecture, and two fossil specimens from the upper middle Miocene Shibiutan Formation of Hokkaido (Figure 1). These specimens are all stored in JUE other than one Narita specimen, which is stored in IGPS. In addition, we also have examined seven right valves and eight left valves of the new form collected from the beach of Peter the Great Bay in Primorye (Figure 1). These are housed in ZMFU. Unfortunately, all materials were empty shells; we could not examine the soft parts.

For comparison with the above specimens, many Recent specimens of *Macoma (Rexithaerus) sector* Oyama were examined from the following localities at hand and stored in IGPS and MNHAH: Katsuori (Ibaraki Pref.); Kagamigaura and Kazusa-Onjuku (Chiba Pref.); Kamakura and Zushi (Kanagawa Pref.); Mikawa-Isshiki (Aichi Pref.); Ise (Mie Pref.); Kushimoto and Shionomisaki (Wakayama Pref.); Ashiya (Fukuoka Pref.); Oga (Akita Pref.); Kakizaki (Niigata Pref.); and Pohang City and Kallam Village (South Korea).

We measured the following characters: shell length, shell height, shell depth, length of pallial sinus (PL) and height of pallial sinus (PH) (see Figure 2).

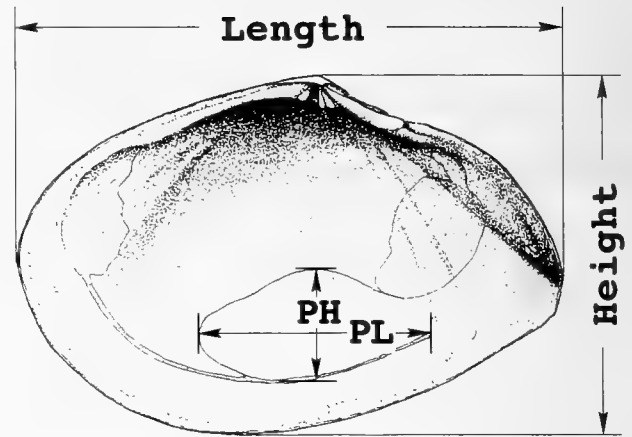


Figure 2. Measurement position.

Description of Northwestern Pacific species

Family Tellinidae de Blainville
Subfamily Macominae Olsson
Genus *Macoma* Leach, 1819

Type species.—*Macoma tenera* Leach, 1819 by monotypy (= *Tellina calcarea* Gmelin, 1791).

Subgenus *Rexithaerus* Tryon, 1869

Type species.—*Tellina secta* Conrad, 1837, by subsequent designation of Dall, 1900.

Macoma (Rexithaerus) hokkaidoensis Amano and Lutaenko
sp. nov.

[Japanese name: Yezo-sagigai]

Figures 3—1-3, 5-6, 8; 4—6

Macoma sector Oyama. Evseev, 1981, pl. 8, figs. 10, 12. [non Oyama, 1950]

Macoma (Rexithaerus) sector Oyama. Kabanov and Lutaenko, 1996, p. 16-18, figs. 2a, c, 5, 6. [non Oyama, 1950]

Type specimens.—JUE no. 15652 (Holotype); JUE no. 15653, 15654 (Paratypes).

Type locality.—Oshamanbe, Hokkaido, Recent.

Description.—Shell of medium size (attaining 63.1 mm in shell length), rather thick, elongate-ovate, inflated, inequilateral, inequivalve; beak situated slightly posteriorly; orthogyrate or weakly opisthocline; posterior commissure line strongly flexed toward right valve; posterior part moderately gaping; periostracum thin, brownish gray in

→ **Figure 3.** 1-3, 5, 6, 8: *Macoma (Rexithaerus) hokkaidoensis* Amano and Lutaenko, sp. nov. 1, 5a-b, 6a-b; JUE no. 15652 (Holotype), Oshamanbe (Recent). 2a-b; IGPS no. 13981, Yamada, Chiba Pref., Narita Formation. 3a-b; ZMFU no. 9324/Bv-220, Gornostay Inlet of Ussuri Bay (Peter the Great Bay; Recent). 8a-b; ZMFU no. 10003/Bv-474, Kievka Bay (60 km east of Nakhodka; Recent). 4, 7: *Macoma (Rexithaerus) sector* Oyama. 4; MIMB no. 2404, Kallam Village near Samchok City, South Korea (Recent). 7a-b; JUE no. 15660, Hossaku, Chiba Prefecture, Narita Formation. All figures natural in size.

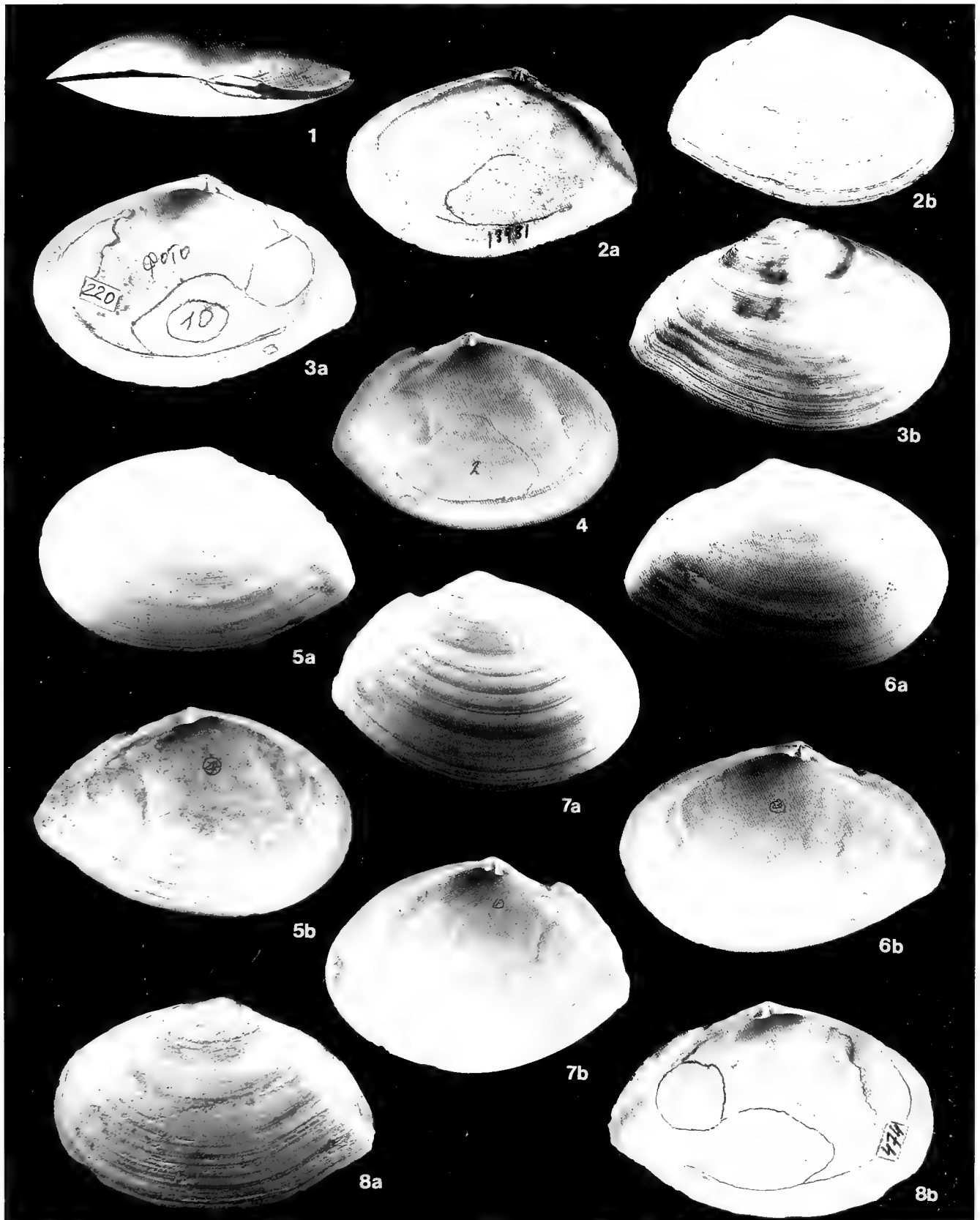
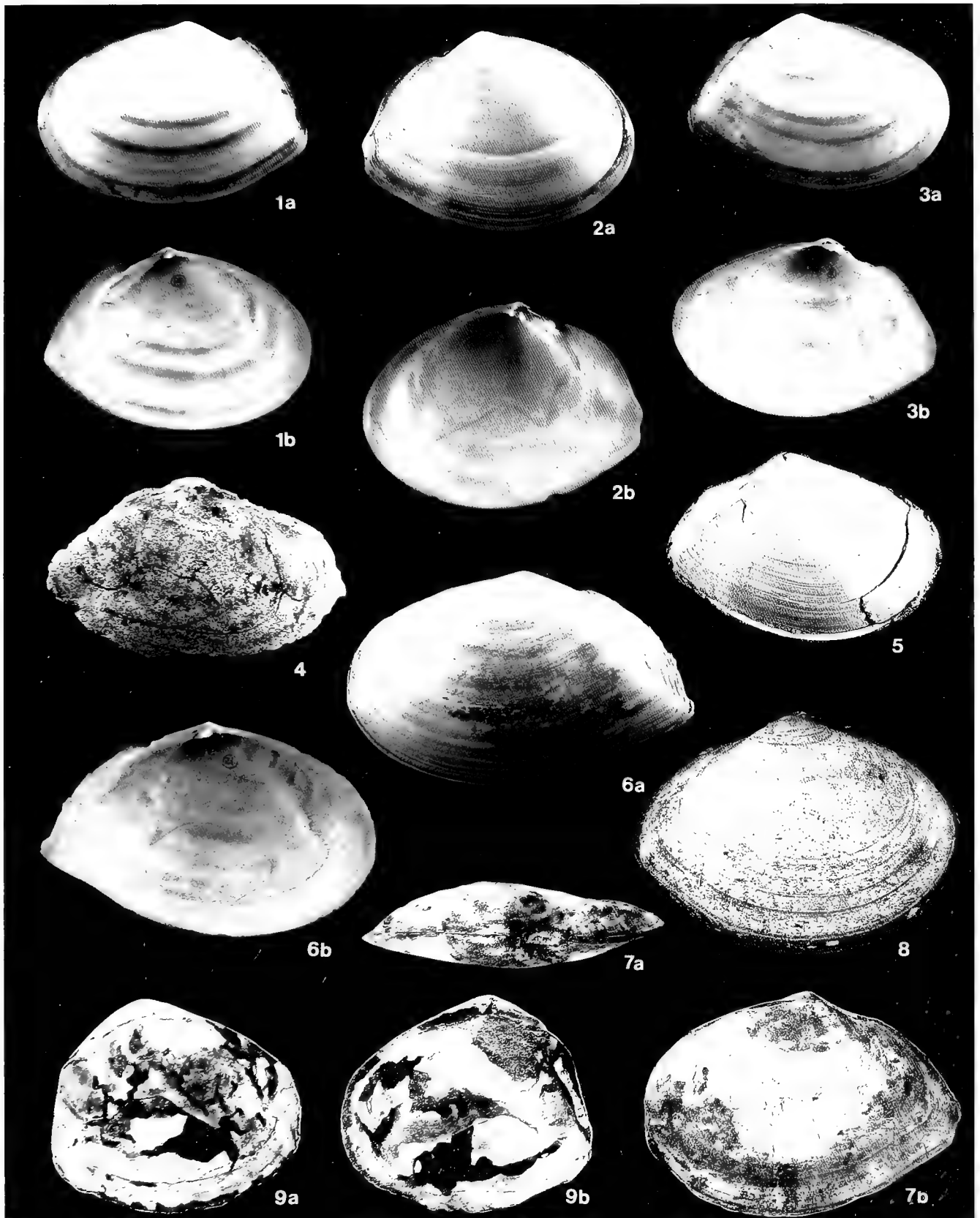


Table 1. Measurements (in mm) of *Macoma (Rexithaerus) hokkaidoensis* Amano and Lutaenko, sp. nov.

| Specimens | Length | Height | PL* | PH* | Valve |
|--------------------------|--------|--------|------|------|-------|
| JUE no. 15652 (Holotype) | 57.4 | 38.0 | 24.5 | 13.0 | Right |
| " | 56.6 | 37.5 | 26.0 | 14.8 | Left |
| JUE no. 15653 (Paratype) | 51.7 | 34.8 | 22.9 | 13.4 | Right |
| JUE no. 15654 (Paratype) | 61.6 | 38.6 | 26.5 | 15.8 | Left |
| JUE no. 15655-1 | 54.4 | 36.4 | 25.1 | 13.3 | Right |
| JUE no. 15655-2 | 50.7 | 32.9 | 23.0 | 12.1 | Right |
| JUE no. 15655-3 | 49.7 | 34.1 | 22.1 | 12.2 | Right |
| JUE no. 15655-4 | 53.5 | 35.2 | 25.1 | 13.5 | Right |
| JUE no. 15655-5 | 53.5 | 34.7 | 22.0 | 12.8 | Right |
| JUE no. 15655-6 | 59.1 | 38.9 | 25.0 | 14.2 | Right |
| JUE no. 15655-8 | 54.9 | 36.8 | 24.5 | 13.7 | Right |
| JUE no. 15655-9 | 63.1 | 40.9 | 29.2 | 15.5 | Right |
| JUE no. 15655-10 | 61.1 | 39.7 | 28.2 | 14.0 | Right |
| JUE no. 15655-11 | 57.5 | 37.0 | 25.0 | 14.1 | Right |
| JUE no. 15655-12 | 51.8 | 35.3 | 24.4 | 14.3 | Right |
| JUE no. 15655-13 | 59.9 | 40.0 | 27.4 | 16.4 | Right |
| JUE no. 15655-14 | 53.4 | 36.2 | 24.2 | 13.9 | Right |
| JUE no. 15655-15 | 48.0 | 32.2 | 23.0 | 13.9 | Right |
| JUE no. 15655-16 | 48.0 | 32.3 | 21.3 | 12.3 | Right |
| JUE no. 15655-17 | 47.8 | 31.1 | 21.1 | 11.8 | Right |
| JUE no. 15655-18 | 42.9 | 28.5 | 19.8 | 11.7 | Right |
| JUE no. 15655-19 | 43.3 | 26.7 | 19.3 | 11.1 | Right |
| JUE no. 15655-22 | 57.5 | 38.1 | 25.0 | 14.0 | Left |
| JUE no. 15655-23 | 57.6 | 36.8 | 25.7 | 15.1 | Left |
| JUE no. 15655-24 | 56.0 | 36.4 | 24.7 | 15.0 | Left |
| JUE no. 15655-25 | 53.9 | 34.5 | 25.9 | 13.9 | Left |
| JUE no. 15655-26 | 50.6 | 33.4 | 24.2 | 14.4 | Left |
| JUE no. 15655-27 | 52.6 | 35.1 | 25.6 | 15.8 | Left |
| JUE no. 15655-28 | 49.4 | 31.9 | 24.0 | 13.6 | Left |
| JUE no. 15655-29 | 46.2 | 29.9 | 22.1 | 11.1 | Left |
| JUE no. 15655-30 | 49.7 | 32.4 | 23.9 | 13.0 | Left |
| JUE no. 15655-31 | 47.2 | 31.6 | 23.2 | 14.3 | Left |
| JUE no. 15655-32 | 47.4 | 30.4 | 24.3 | 14.2 | Left |
| JUE no. 15655-33 | 46.9 | 30.2 | 23.0 | 12.2 | Left |
| JUE no. 15655-34 | 41.7 | 27.4 | 20.2 | 11.6 | Left |
| JUE no. 15656-1 | 36.6 | 24.6 | 16.1 | 9.2 | Right |
| " | 36.7 | 23.9 | 18.2 | 10.1 | Left |
| JUE no. 15656-2 | 56.0 | 37.2 | 27.1 | 14.8 | Left |
| ZMFU no. 220 | 56.1 | 38.8 | 26.9 | 15.3 | Right |
| ZMFU no. 1621 | 44.1 | 30.2 | 21.8 | 12.3 | Right |
| ZMFU no. 1553 | 42.3 | 29.1 | 21.3 | 10.3 | Right |
| ZMFU no. 23407 | 60.4 | 40.0 | 28.5 | 16.6 | Left |
| ZMFU no. 474 | 56.9 | 39.2 | 26.2 | 15.5 | Right |
| " | 56.1 | 39.1 | 26.7 | 15.9 | Left |
| ZMFU no. 1215 | 42.1 | 28.3 | 20.9 | 11.5 | Left |

* PL=length of pallial sinus; PH=height of pallial sinus. See Fig. 2.

→ **Figure 4.** 1, 3, 5: *Macoma (Rexithaerus) sector* Oyama. 1a-b, 3a b; JUE no.15657, Zushi, Kanagawa Prefecture (Recent). 5; JUE no. 15661, Kakuma, Ishikawa Prefecture, Omma Formation. **2a b:** *Macoma (Rexithaerus) secta* (Conrad); JUE no. 15662, Monterey Bay, California (Recent). **4:** *Macoma (Rexithaerus) cf. hokkaidoensis* Amano and Lutaenko, sp. nov.; JUE no. 15659, Kami-tokushibetsu, Hokkaido, Shibiutan Formation. **7-9:** *Macoma (Rexithaerus) shiratoriensis* (Matsubara). 7a-b, 9a-b; IGPS no. 102563 (Paratypes), Shiratori, Iwate Prefecture, Kadonosawa Formation. 8; IGPS no. 102562 (Holotype), Shiratori, Iwate Prefecture, Kadonosawa Formation. All figures natural size.



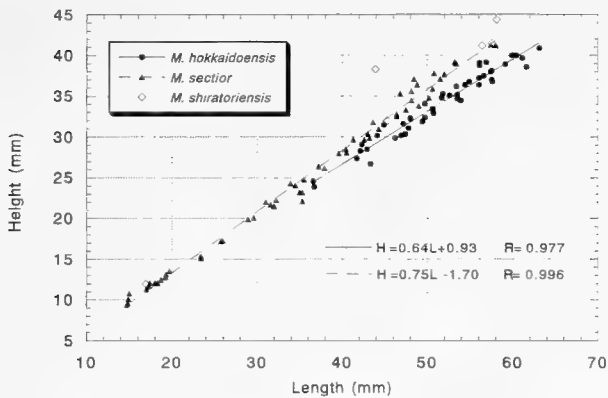


Figure 5. Relation between shell length and shell height.

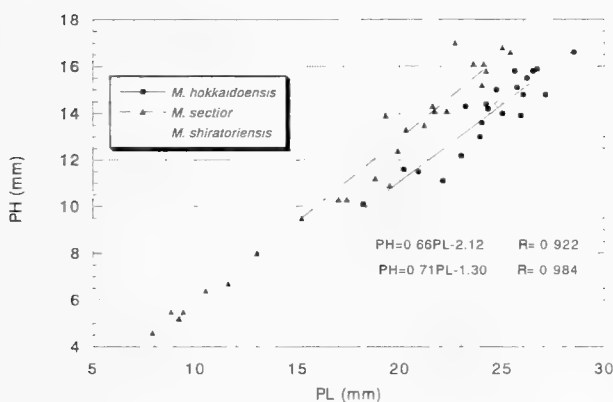


Figure 6. Relation between length of pallial sinus (PL) and height of pallial sinus (PH) of left valve.

color; nymph short, produced.

Right valve moderately inflated; a strong ridge running from beak to posterior corner; area in front of ridge distinctly concave, especially near ventral margin; anterodorsal margin broadly arcuate; posterodorsal margin behind ligament upwardly elevated forming dorsal flange; posterior margin obliquely truncated; anterior muscle scar elongated oblong and its inner margin undulated; posterior muscle scar subovate; pallial sinus deep, low ovate in shape, and slightly concave between highest and deepest end of pallial sinus; hinge plate rather wide; anterior cardinal tooth thin and smooth; posterior cardinal tooth large and subdivided by a distinct groove.

Left valve less inflated; a very weak ridge running from beak to posteroventral corner; a shallow groove running along just posterior part of ridge; anterodorsal margin broadly arcuate; posterodorsal margin behind ligament slightly upwardly elevated forming dorsal flange; posterior margin obliquely subtruncated; ventral margin broadly arcuate and excavated just before posteroventral corner; posteroventral corner bluntly pointed; anterior muscle scar deeply impressed, elongated oblong and its inner margin undulated; posterior muscle scar subcircular; pallial sinus deep, but low ovate in shape; anterior cardinal tooth elevated and sub-

divided by deep groove; posterior cardinal tooth very thin, inclined posteriorly and smooth.

Remarks.—The present species had already been illustrated as *Macoma sector* Oyama from the Primorye region (Holocene and Recent), Russia (Evseev, 1981; Kafanov and Lutaenko, 1996). The previously figured specimens have a transversely elongate shell, obliquely truncated posterodorsal margin, less prominent dorsal flange, and low pallial sinus shape. Based on these characteristics, they are referred to the present new species.

Rexithaerus cf. *sector* (Oyama) was recorded from the Middle Miocene Shibiutan Formation of northeastern Hokkaido by Fujimoto *et al.* (1998). Some specimens at hand (e.g. JUE no. 15659, see Figure 4—4) from this formation have an elongated shell with obliquely truncated posterior margin, a strong posterior ridge and low ovate pallial sinus, which are in common with the new species. However, it is difficult for them to be exactly identified with *Macoma (Rexithaerus) hokkaidoensis* because the shell material had eroded out. Thus, we compare the specimens from the Shibiutan Formation with the present new species.

Comparison.—The living species, *Macoma (Rexithaerus) sector* Oyama, 1950, differs from *M. (R.) hokkaidoensis* by having a less elongated shell (Table 1; Figure 5), higher pallial sinus of both right and left valves (Figure 6), vertically truncated posterior margin, no concave area in front of the posterior ridge, a narrower hinge plate and a prominent dorsal flange. It is especially easy to distinguish the left valves of the two species by the shapes of the posterior part and pallial sinus.

Macoma (Rexithaerus) shiratoriensis was described from the uppermost lower to lower middle Miocene Kadonosawa Formation in Iwate Prefecture by one of the authors (Matsumura, 1994). This species closely resembles the present new one in its low pallial sinus (Figure 6), less prominent flange and obliquely truncated posterior margin. However, the straight line between the deepest and highest points of the pallial sinus, the higher shell and the concave area in front of the posterior ridge distinguish *M. (R.) shiratoriensis* from the present new species.

Macoma (Rexithaerus) indentata Carpenter, 1864, a Recent species of Northwest America, is similar to the present new species in its protruded posterior part and its elongated shell form. However, it is easy to distinguish the two species by comparing the pallial sinus shape. *M. (R.) indentata* has a much higher pallial sinus than *M. (R.) hokkaidoensis*. Moreover, *M. (R.) indentata* has a more elongate shell with a distinct depressed area in the posteroventral part of the shell, and a bill-like posterior end. Right valve of *M. (R.) indentata* has a pronounced flexure of gully-like type on the surface much deeper than in *M. (R.) hokkaidoensis*.

Macoma (Rexithaerus) indentata flagleri Etherington, 1931, described from the lower middle Miocene Astoria Formation of Washington, is an allied subspecies in its shell outline. However, *M. (R.) i. flagleri* lacks the pointed posteroventral corner. Unfortunately, we could not compare the internal shell characters of this subspecies because no description of the interior of the shell has been published.

Measurements (in mm).—See Table 1.

Distribution.—Late middle Miocene : Shibiutan Formation of Hokkaido (cf.). Pleistocene : Narita Formation in Chiba Prefecture. Recent : Oshamanbe and Yufutsu in Hokkaido, Aniva Bay in Sakhalin, Kunashiri Is., Peter the Great Bay and Ussuri Bay in Primorye, Russia.

***Macoma* (*Rexithaerus*) *sector* Oyama, 1950**

[Japanese name : Sagigai]

Figures 3—4, 7 ; 4—1, 3, 5

Macoma secta (Conrad). Yokoyama, 1922, p. 143–144, pl. 11, fig. 1 ; Nomura, 1938, p. 263–264, pl. 36, figs. 5, 6. [non Conrad, 1837]

Macoma (*Rexithaerus*) *sector* Oyama, 1950, p. 3 ; Kira, 1954, p. 160, pl. 60, fig. 26 ; Yamamoto and Habe, 1959, p. 106, pl. 9, figs. 1, 2 ; Kaseno and Matsuura, 1965, pl. 17, figs. 10, 11 ; Habe and Kosuge, 1967, p. 163, pl. 61, fig. 24 ; Ohara, 1971, pl. Q–10, figs. 5a–b ; Habe, 1977, p. 210, pl. 42, figs. 11, 12 ; Matsuura, 1985, pl. 42, fig. 15 ; Fujii and Shimizu, 1991, pl. 1, fig. 20 ; Fukuda *et al.*, 1992, p. 91, pl. 34, fig. 538 ; Izawa and Matsuoka, 1996, p. 8, pl. 6, fig. 9.

Macoma hokiensis Akutsu, 1964, p. 287–288, pl. 60, fig. 8.

Rexithaerus sector Oyama. Chiba-ken Chigaku Kyoiku Kenkyu-kai, 1968, pl. 12, figs. 10a–b ; Kuroda *et al.*, 1971, p. 697 (in Japanese), p. 458–459 (in English), pl. 100, fig. 5 ; Oyama, 1973, p. 113, pl. 52, figs. 14a–b ; Ogasawara, 1977, p. 122–123, pl. 14, figs. 5a–b, 7 ; Koyama *et al.* eds., 1981, p. 134 ; Ogasawara *et al.*, 1986, pl. 74, figs. 9a–b ; Ishii, 1987, p. 14, pl. 12, figs. 12a–b ; Baba, 1990, p. 289 ; Baba, 1992, p. 540, pl. 69, fig. 11 ; Matsubara, 1994, pl. 2, figs. 6a–b, 7a–b.

Macoma sector Oyama. Okutani and Habe, 1983, p. 139, 215 ; Nemoto and Akimoto, 1990, p. 42, pl. 11, fig. 7 ; Kondo, 1991, fig. 3–4.

Macoma (*Rexithaerus*) *sector* (Oyama). Kwon *et al.*, 1993, p. 379, figs. 91–6–1, and 91–6–2.

Macoma "*hokiensis*" Akutsu. Matsubara, 1994, pl. 2, fig. 5.

non *Macoma sector* Oyama. Evseev, 1981, pl. 8, figs. 10, 12. [= *Macoma* (*Rexithaerus*) *hokkaidoensis* sp. nov.]

non *Rexithaerus sector* Oyama. Ogasawara, 1981, pl. 1, fig. 9. [= *Macoma* (*Macoma*) *tokyoensis* Makiyama, 1927]

non *Rexithaerus sector* (Oyama). Ogasawara and Naito, 1983, pl. 7, fig. 3. [?= *Macoma* (*Macoma*) *tokyoensis* Makiyama, 1927]

non *Macoma* (*Rexithaerus*) *sector* Oyama. Kafanov and Lutaenko, 1996, p. 16–18, figs. 2a, c, 5, 6. [= *Macoma* (*Rexithaerus*) *hokkaidoensis* sp. nov.]

Type specimen.—UMUT CM21317 (Lectotype, designated herein).

Type locality and Formation.—Otake, Narita City, Chiba Prefecture, Narita Formation, Pleistocene.

Original description.—"Macoma *secta*" in North America has a large, very high, rather thick shell, which is similar to *Nuttallia* in shape. On the other hand, the shell of the present new species [*M. (R.) sector*] is normal in shape, low, thin, fragile, and does not attain a large size. Posterior ridge of American species is highly elevated while that of the present new species is rather weak. Inner side of posterior end of ligament becomes strongly thickened in American species, whereas that of the present new species does not. Posterior adductor muscle scar is situated rather near beak,

and a contacting point between pallial line and sinus is separated from anterior adductor muscle scar. The type specimen was collected from Sagami Bay (Enoshima)." (translated from the Japanese original description)

Remarks.—Although Oyama (1950) designated the type locality of the present species as Enoshima in Kanagawa Prefecture, he neither designated nor illustrated the type specimen. In addition, the depository still remains unknown.

However, Oyama (1950) did list *Macoma secta* of Yokoyama (1922) as a synonym. Consequently, we designate herein the specimen illustrated as *Macoma secta* by Yokoyama (1922) as the lectotype. This specimen is registered in the University Museum of the University of Tokyo as CM21317 (Oyama, 1973).

Macoma hokiensis Akutsu, 1964, described from the Kanomatazawa Formation in Tochigi Prefecture, is regarded as synonymous with the present species on the basis of its rather high shell and pallial sinus shape (see pl. 2, fig. 5 of Matsubara, 1994).

Macoma secta (Conrad) by Otuka (1940), from the lower middle Miocene Wakkauensetsu Formation of Hokkaido, was recently considered as synonymous with *M. (R.) sector* Oyama by Kafanov and Lutaenko (1996). However, at least the specimen shown in pl. 11, fig. 1 of Otuka (1940) is not referable to the subgenus *Rexithaerus* because of its rounded posterior margin and the absence of a posterior ridge.

Macoma izurensis illustrated by Masuda and Takegawa (1965), from the Fukuda Formation in Miyagi Prefecture, much resembles the present species in the pallial sinus shape rather than either *M. (R.) hokkaidoensis* or *M. (R.) shiratoriensis*. However, it differs in having a more obliquely truncated posterodorsal margin. Thus, we treat the specimens of Masuda and Takegawa (1965) as *M. (R.) aff. sector* Oyama, although they were questionably referred to *M. (R.) shiratoriensis* by Matsubara (1994).

Comparison.—The present species closely resembles *Macoma* (*Rexithaerus*) *secta* (Conrad, 1837) (Fig. 4—2) known from the western coast of North America. However, *M. (R.) sector* is distinguished from *M. (R.) secta* by having a smaller, lower, less inflated shell.

Distribution.—Late middle or early late Miocene : Kanomatazawa Formation in Tochigi Prefecture (Akutsu, 1964). Pliocene : Tatsunokuchi Formation in Miyagi Prefecture (Nomura, 1938) ; Mita Formation in Toyama Prefecture (Matsuura, 1985 ; Fujii and Shimizu, 1991). Early Pleistocene : Omma Formation in Ishikawa Prefecture (Kaseno and Matsuura, 1965 ; Ogasawara, 1977 ; Matsuura, 1985) ; Haizume Formation in Niigata Prefecture (this study) ; Nakatsu Group in Kanagawa Prefecture (Baba, 1992). Middle to late Pleistocene : Nagahama Formation in Chiba Prefecture (Baba, 1990) ; Narita Formation in Chiba Prefecture (Yokoyama, 1922 ; Chiba-ken Chigaku Kyoiku Kenkyu-kai, 1968 ; Oyama, 1973 ; Baba, 1990) ; Kioroshi Formation (?) in Chiba Prefecture (Kondo, 1991) ; Semata Formation in Chiba Prefecture (Ohara, 1968) ; Uji Shell Bed in Ishikawa Prefecture (Matsuura, 1985) ; Anden Formation in Akita Prefecture (Ogasawara *et al.*, 1986). Holocene : Yokohama in Kanagawa Prefecture (Matsushima, 1969) ; Osaka in Osaka Prefecture

(Ishii, 1987); Anan in Tokushima Prefecture (Nakao, 1995). Recent: Honshu, Shikoku, Kyushu and South Korea (Higo and Goto, 1993); ? Formosa (Taiwan) (Kuroda, 1941; Wu, 1980).

Macoma (Rexithaerus) shiratoriensis (Matsubara, 1994),
combin. nov.

[Japanese name: Shiratori-sagigai]

Figures 4–7–9

Macoma cf. *tokyoensis* Makiyama. Ogasawara, 1973, pl. 13, fig. 4. [non Makiyama, 1927]

Macoma aomoriensis Nomura. Ogasawara, 1973, pl. 13, fig. 9. [non Nomura, 1935]

Macoma izurensis (Yokoyama). Ogasawara *et al.*, 1986, pl. 1, figs. 12, 13. [non Yokoyama, 1925]

Macoma sp. B. Ogasawara and Morita, 1986, pl. 2, figs. 25, 28. *Rexithaerus shiratoriensis* Matsubara, 1994, p. 24–27, tab. 1, pl. 1, figs. 1, 2, 3a–c, 4a–c, 5a–b, pl. 2, figs. 1a–c, 2, 3, 4.

Type specimen.—IGPS no. 102562 (Holotype), 102563–1 to –10 (Paratypes).

Type locality.—A small tributary of the Shiratorigawa River, south of Shiratori, Ninohe City, Iwate Prefecture.

Remarks.—The present species is characterized by its moderate-sized (maximum length 61.4 mm), transversely elongate-ovate shell (height/length 0.71 to 0.79) with a rather weakly developed posterior ridge, less elevated dorsal flange, obliquely subtruncated posterodorsal margin and low pallial sinus.

All species questionably listed by Matsubara (1994), *Macoma* cf. *tokyoensis* and *Macoma aomoriensis* of Ogasawara (1973), and *Macoma izurensis* of Ogasawara *et al.* (1986), from the same locality belonging to the Nishikurosawa Formation in Akita Prefecture, are considered to be synonymous with the present species. On the other hand, *Macoma izurensis* of Kamada (1962), from the Honya and Nakayama Formations in Fukushima Prefecture, is not referred to the present species. As a result of the reexamination of the hypotypes, it becomes clear that the flange-like posterodorsal margin in the figures of Kamada (1962) is not original, but is due to matrix covering shell material. Thus, these specimens are referred to *Macoma (Macoma) izurensis* (Yokoyama, 1925) as Kamada (1962) thought.

Macoma sp. B of Ogasawara and Morita (1986) from the middle Miocene Yanagawa Formation in Fukushima Prefecture is considered to be *M. (R.) shiratoriensis* based on its transversely elongate ovate shell with obliquely truncated posterodorsal margin.

Comparison.—*M. (R.) shiratoriensis* closely resembles *M. (R.) indentata flagleri* Etherington, 1931. However, the former species can be distinguished from the latter subspecies by having a larger shell with less distinct growth lines and less developed posterior ridge. As already mentioned, the internal characteristics of *M. (R.) indentata flagleri* are unavailable and thus an exact comparison is difficult.

The present species is easily distinguished from *M. (R.) indentata indentata* Carpenter, a Recent northeastern Pacific species, by having a weaker ridge, less protruding posterior

margin, less compressed posteroventral margin in front of a ridge, and lower pallial sinus.

Distribution.—Latest early Miocene: Kadonosawa Formation in Iwate Prefecture (Matsubara, 1994). Latest early–early middle Miocene Nishikurosawa Formation in Akita Prefecture (Ogasawara, 1973; Ogasawara *et al.*, 1986). Early middle Miocene: Yanagawa Formation in Fukushima Prefecture (Ogasawara and Morita, 1986).

Temporal and spatial distributions of *Macoma (Rexithaerus)* in Northwest Pacific

The subgenus *Rexithaerus* was considered to be one of those elements which originated in northwestern North America in late Oligocene and migrated into the Northwest Pacific by the late early Miocene (Matsubara, 1994). The earliest *Rexithaerus* species in the Northwest Pacific region; *M. (R.) shiratoriensis* (Matsubara), occurs from the upper lower to lower middle Miocene in formations in northeastern Honshu (Figure 7). According to the climato-paleogeographic map of Ogasawara (1994), this species lived in the subtropical realm, but could not invade the tropical one.

The next fossil occurrence is *M. (R.)* cf. *hokkaidoensis* from the upper middle Miocene Shibiutan Formation of Hokkaido, described above. According to Fujimoto *et al.* (1998), the molluscan assemblage including *M. (R.)* cf. *hokkaidoensis* is correlated with the upper sublittoral “Pitar”–*Anadara* Assemblage of the Lower Togheshita fauna (Amano, 1983, 1986). This fauna occupied the mild- or cool-temperate realm in the middle Miocene of Hokkaido (Ogasawara *et al.*, 1993; Ogasawara, 1994).

On the other hand, the earliest fossil record of *Macoma (Rexithaerus) sector* Oyama is known from the Kanomata-

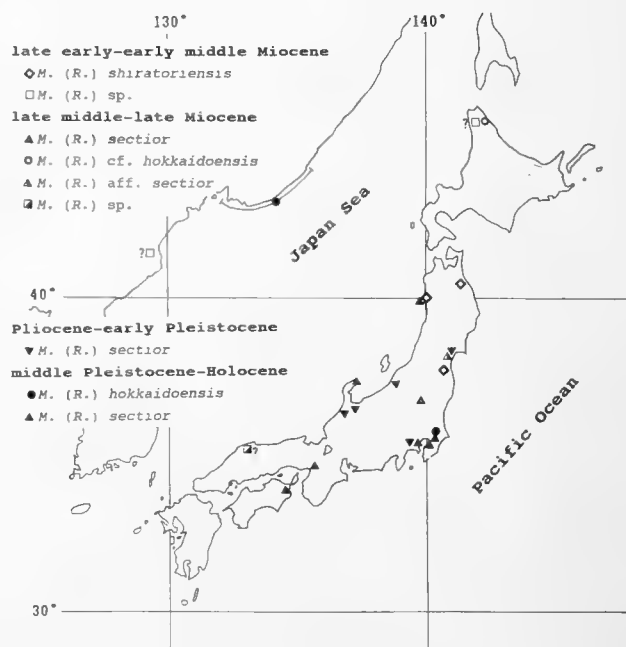


Figure 7. Distribution of the fossil *Macoma (Rexithaerus)*.

zawa Formation in Tochigi Prefecture (Akutsu, 1964, as *Macoma hokiensis*). The age of the horizon bearing this species is somewhere between the N. 14 and N. 16 zones of the late middle to early late Miocene based on the planktonic foraminiferal data (Saito, 1963; Otsuki and Kitamura, 1986). According to Ogasawara (1994), the Kanomatazawa Formation was deposited in the warm-temperate realm. *Macoma secta* (Conrad) was recorded from the lower middle Miocene Ilyinskaya and the upper Miocene Ermanovskaya Formations in Kamchatka by Sineknikova (1976) and Gladenkov *et al.* (1984). However, these are referred to *Macoma* s.s. because the specimens lack the posterior ridge.

Pliocene *M. (R.) sector* is recorded in the cool- to mild-temperate realm. This species was described from the Tatsunokuchi Formation in Miyagi Prefecture (Nomura, 1938), whose age is the latest Miocene to early Pliocene (Yanagisawa, 1990, 1998). On the other hand, *M. (R.) sector* was also illustrated by Fujii and Shimizu (1991) from the Mita Formation in Toyama Prefecture.

Early Pleistocene records of *M. (R.) sector* Oyama exist from the Omma-Manganji fauna recognized in the Japan Sea borderland in central and northern Japan. The distribution of this species is restricted to the Omma-Manganji (proper) and Kanto-type subprovinces of Ogasawara (1986), both of which correspond to the mild-temperate marine climate (Ogasawara, 1994). Thus, *M. (R.) sector* in the early Pleistocene was confined to the mild-temperate water.

In the Recent, *M. (R.) hokkaidoensis* lives in the cool-temperate and subarctic shallow waters in Hokkaido, south Sakhalin, south Kurile Islands and Primorye while *M. (R.) sector* Oyama lives in the upper sublittoral (10–30 m in depth) of the mild-temperate to subtropical waters around Honshu, Kyushu, Shikoku, and South Korea (Higo and Goto, 1993).

After the subgenus *Rexithaerus* arrived in the northwestern Pacific, it lived in the subtropical realm during the late early to early middle Miocene, or the so-called "Climatic Optimum" age. By the late middle Miocene, the subgenus had adapted to the temperate zone as climates cooled after the "Climatic Optimum". From the late middle Miocene to the Plio-Pleistocene, the subgenus *Rexithaerus* lived in the mild- or cool-temperate realm. In the Holocene, *M. (R.) sector* extended its range to subtropical waters. Kuroda (1941) and Wu (1980) only listed *M. (R.) sector* from Formosa (Taiwan). If this is true, *M. (R.) sector* may live in the tropical water. However, there is no illustration of the Formosa specimen.

The muricid gastropod genus *Ceratosoma*, a member of the westward-spreading group, shows a history of expansion similar to that of *Rexithaerus*. Both *Macoma* (*Rexithaerus*) and *Ceratosoma* invaded the subtropical waters around Japan by the early middle Miocene and adapted to the cool- to mild-temperate zone by the early Pleistocene. After or during the middle to late Pleistocene, their distribution extended southward to subtropical waters (Amano and Vermeij, 1998). On the other hand, one of the same westward-spreading muricids, *Nucella*, only lives in mild-temperate to arctic waters (Higo and Goto, 1993). One plausible reason why *Nucella* did not invade warmer waters may be related to its original adaptation not to the subtropical water as *Macoma* (*Rexithaerus*) or *Ceratosoma*, but to the cool-

temperate water around Japan in the early middle Miocene (Amano *et al.*, 1993).

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The turrilitid ammonoid *Mariella* from Hokkaido — Part 1

(Studies of the Cretaceous ammonites from Hokkaido and Sakhalin—LXXXV)

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Abstract. Three species of the genus *Mariella* (Turrilitidae) from the Lower Cenomanian (Cretaceous) of Hokkaido are described. They include the two widespread species, *M. (M.) dorsetensis* (Spath, 1926) and *M. (M.) oehlerti* (Pervinquière, 1910). The third species, *M. (M.) pacifica* sp. nov., is somewhat similar to but distinguished from *M. (M.) oehlerti*. It is also compared with some other species. The problem of dimorphism in the turrilitid ammonoids is discussed.

Key words : Cenomanian, dimorphism, Hokkaido, *Mariella*, Turrilitidae

Introduction

Ammonoids of the family Turrilitidae have been recorded from various regions of the world. They occur in the mid Cretaceous (Albian and Cenomanian) and include a number of widespread species which are useful for biostratigraphic zonation and correlation. Some of them are, however, apparently endemic. Turrilitids would be also useful to investigate some aspects of palaeogeography and palaeoenvironments during mid-Cretaceous times.

Aside from several stratigraphic papers in which some turrilitid species are listed or briefly mentioned, very few species have been hitherto described from Japan, although such a magnificent example as *Turrilites komotai* Yabe, 1904 (p. 7, pls. 1, 2) [now referred to *Hypoturrilitis*] was once reported. In our present knowledge ammonoids of the Turrilitidae occur fairly commonly in the mid-Cretaceous sediments of certain biofacies in Hokkaido. A rare but important occurrence of *Mesoturrilitis* from Hokkaido has been recently reported (Matsumoto and Inoma, 1999). More species of the family are to be described successively. In this paper three species of the genus *Mariella* are described, of which two are well known and widespread. The third species is regarded as new and has not been known elsewhere.

Incidentally, T. M. had opportunities to examine some specimens at the Natural History Museum, London, and several other overseas institutions. Moreover, W. J. Kennedy kindly sent several specimens to Kyushu University as reference material.

Geographic and stratigraphic setting

The specimens dealt with in this paper were obtained mainly from the Soeushinai area [Shumarinai–Soeushinai area by some authors] of the Teshio Mountains, northwestern Hokkaido. The Cretaceous strata are exposed in the Shumarinai Valley, the Sounnai Valley and the smaller rivulets, such as the Kyoei–Sakin–zawa and the Sanjussen–zawa, which are all tributaries of the River Uryu, and also in the upper reaches of the River Kotanbetsu. This area was geologically mapped by Hashimoto *et al.* (1965) and has been recently reinvestigated by Nishida *et al.* (1992, 1993, 1996, 1997, 1998a, 1998b). The localities where megafossils and microfossils were collected are pinpointed in the papers by Matsumoto and Inoma (1975) and Inoma (1980) and, furthermore, in a number of route maps of the stratigraphic papers by Nishida *et al.* (1992, 1993, 1996–1998a, b). Moreover, a locality guide is to be given as an Appendix to this paper.

As has been clarified by the above authors, a thick series of strata comprehensively called the Middle Yezo Subgroup of late Albian through Turonian age is extensively distributed in this area. The conformably underlying Lower Yezo Subgroup and the transitionally overlying Upper Yezo Subgroup are partly observable in the area. In a revised scheme of Nishida *et al.* (1996, fig. 10) the Middle Yezo Subgroup in this area is lithostratigraphically subdivided into the Members My1 to My8 in ascending order. The Members My1 and My2, together with the uppermost portion of the Lower Yezo Subgroup, are Upper Albian, the Member My3 is Lower Cenomanian, and the Members My4 and My5 represent the rest of the Cenomanian. The age correlation is based on the assemblage of ammonoid and inoceramid species and also on that of some microfossils (Nishida *et al.*,

1992, 1993, 1996–1998a, b). As there is a lateral change in the lithofacies and thickness of the members from place to place, boundary planes of the successive members may be somewhat diachronous in some cases.

The turrilitid ammonoids have been obtained from the Members My2, My3 (most commonly) and My5 and also the upper part of the Lower Yezo Subgroup. These members consist primarily of mudstones, which are sometimes sandy or have intercalated sandy layers and laminae.

Conventions

Repository.—The illustrated and/or measured specimens are registered in the following institutions which are indicated by the abbreviated symbols as follows:

- GK : Type Room, Department of Earth and Planetary Sciences, Kyushu University, Hakozaki, Fukuoka
- GS : Geological Collections, Faculty of Culture and Education, Saga University, Saga
- MCM : Mikasa City Museum, Mikasa, Hokkaido
- TKD : Institute of Geosciences, Tsukuba University, Tsukuba [reconstitution of the Tokyo Kyoiku Daigaku]
- UMUT : University Museum, University of Tokyo, Hongo, Tokyo

Morphological terms.—For the morphological terms to describe the turrilitid ammonoids, we follow those used by Wright and Kennedy (1996). Setting the apex of the turrilid shell at the top, the terms upper and lower or adapical and adoral [=abapical] are defined and the rows of tubercles or ribs on the face of each whorl are described in descending order as the first, the second and so on. The term flank (see Förster, 1975) may be used for the exposed whorl face of

Wright and Kennedy (1996).

Palaeontological descriptions

Order Ammonoidea Zittel, 1884
 Suborder Ancyloceratina, Wiedmann, 1966
 Family Turrilitidae Gill, 1871
 Genus *Mariella* Nowak, 1916

Type species.—*Turrilites bergeri* Brongniart, 1822 (p. 395, pl. 7, fig. 3) by original designation (Nowak, 1916, p. 10).

Remarks.—Wright and Kennedy (1996, p. 330) have given an ample generic diagnosis and discussed problems of nomenclature. The genus includes the two subgenera, *Mariella* (*Mariella*) Nowak, 1916 and *Mariella* (*Wintonia*) Adkins, 1920, the latter of which is a senior synonym of *Mariella* (*Plesiotturrilites*) Breistroffer, 1953 (see Wright and Kennedy, 1996, p. 331). An undoubted example of *M.* (*Wintonia*) has not been so far found from Japan, whereas there are a number of specimens from Hokkaido which are referable to at least eight species of *M.* (*Mariella*).

Mariella (*Mariella*) *dorsetensis* (Spath, 1926)

Figure 1

Turrilites bergeri Brongniart. Sharpe, 1857, p. 65, pl. 26, fig. 11 only.

Turrilites dorsetensis Spath, 1926, p. 429.

Mariella dorsetensis (Spath). Spath, 1937, p. 513; Marcinowski, 1970, p. 431, pl. 3, fig. 1; Seyed-Emami and Aryai, 1981, p. 26, pl. 6, figs. 5, 6.

Paraturrilites lewesiensis (Spath). Benavides-Cáceres, 1956, p. 436 (pars.), pl. 40, figs. 8, 9 (?).

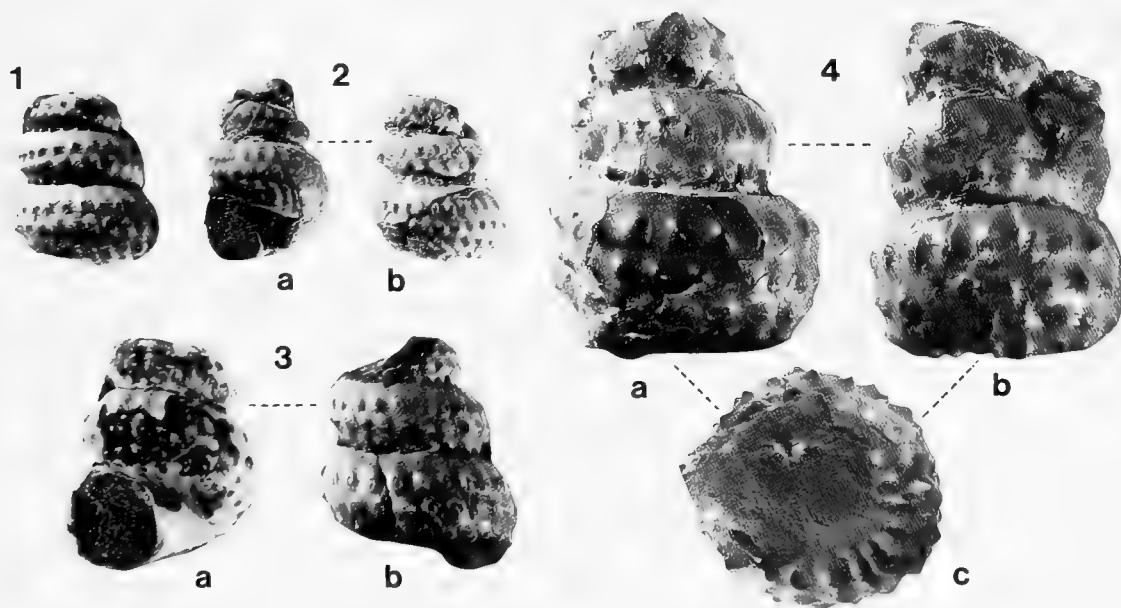


Figure 1. *Mariella* (*Mariella*) *dorsetensis* (Spath). 1. GS. 180, $\times 1$. 2a, b. GK. H8504, two lateral views, $\times 2$. 3a, b. GS. G180, two lateral views (different sides from 1), $\times 2$. 4a–c. GS. G182, two lateral and basal views, $\times 1.5$.

Mariella (Mariella) dorsetensis (Spath). Atabekian, 1985, p. 35, pl. 6, figs. 6, 9; Wright and Kennedy, 1996, p. 344, pl. 100, figs. 5, 11, 17, 19, 22, 25; pl. 102, fig. 7; text-figs. 136B, E (with full synonymy).

Holotype.—BMNH. C3834, figured by Sharpe, 1857, pl. 26, fig. 11 and named as *Turrilites dorsetensis* Spath, 1926, p. 429 (by monotypy).

Material.—GS. G180 (Figure 1-1, 3) and GS. G181, both from loc. R905 [=YKC080621b], Hotei-zawa; GK. H8504 (Figure 1-2) from loc. R518p5, East Suribachi-zawa; GK. H8505 from loc. R438p, GK. H8506 from loc. R433p, and TKD 30081A, B from loc. 81007, in the upper reaches of the Suribachi-zawa; TKD 30080A-D from loc. 71204 in the middle course of the River Shumarinai; GS. G182 (Figure 1-4), from loc. YKC060824, Sanjussen-zawa. These are all from the Lower Cenomanian Member My3 of the Soeushinai area.

Description.—The available specimens are all small and incomplete, as seen in the illustration (Figure 1). In general, the apical angle is acute (20–25° in our estimation). The whorl is rounded in section, showing a moderately or broadly convex outer face; the whorl junction is well defined and crenulated.

The tubercles in four rows are of moderate density and number 20 to 25 per whorl in each row. The tubercles on the outer whorl face are disposed slightly obliquely in three rows at subequal intervals and of nearly equal moderate intensity. The tubercle of the first row is elongated upward to a distinct rib on the upper face of the whorl. In some specimens the fourth tubercle is slightly smaller than the others and close to the third one, although it is beyond the lower whorl seam. On the lower whorl face ribs run from the third row tubercles to the narrow umbilicus by way of the fourth row tubercles, showing a gentle curvature.

Septal sutures are partly exposed (GK. H8505).

Comparison.—The above-described specimens from Hokkaido are well comparable with the holotype and other examples of *M. (M.) dorsetensis* from England (Wright and Kennedy, 1996, pl. 100, figs. 5, 11, 17, 19, 22, 25) and also previously illustrated specimens from several regions of the world (see synonymy list). Affinities with other allied species are discussed below, together with some remarks on questionable points.

Occurrence.—As for material. This species has been reported from the Lower Cenomanian of southern England, northern France, Poland, Turkmenistan, Iran, Madagascar and Peru (see synonymy list).

Discussion.—*M. (M.) dorsetensis* is similar to and could be interpreted as a descendant from *M. (M.) bergeri* of the uppermost Albian. The apical angle of the former is smaller than that of the latter. In fact the apical angle of *M. (M.) bergeri* is recorded as 33–38° by Spath (1937, p. 511) and an example of Pictet and Campiche (1862, pl. 58, fig. 2) reillustrated by Renz (1968, pl. 18, fig. 4) gives 34°, as compared to the 20–25° of *M. (M.) dorsetensis*. On the average the tubercles are somewhat more crowded and more distinctly connected by longitudinal ribs in *M. (M.) bergeri*.

The relationship between *M. (M.) dorsetensis* and *M. (M.)*

lewesiensis (Spath, 1926) is a moot problem, as has been discussed by Kennedy (1971, p. 28) and Klinger and Kennedy (1978, p. 31). The difficulty can be guessed from the confused state in the lists of synonymy between authors (even between the same palaeontologist writing on different dates) (see Wright and Kennedy, 1996, p. 339–340 and p. 344). Collignon (1964, pl. 331, fig. 1482) has shown an example of *M. (M.) dorsetensis* with a rostrate last whorl. This suggests the small size of this species. We notice, however, that an example of the same species illustrated by Atabekian (1985, pl. 6, fig. 6, 6b) is nearly as large as the holotype of *M. (M.) lewesiensis* (see Sharpe, 1857, pl. 20, fig. 10 or Wright and Kennedy, 1996, p. 101, fig. 3). There is no difference in the estimated apical angle between the two species. There may be differences in the ornament. The relative smoothness of the upper face of the whorl was regarded as a criterion by which to distinguish *M. (M.) lewesiensis* from *M. (M.) dorsetensis*, but some of the coarse tubercles of the first row in the former show faint elongations on a part of the upper whorl face, depending probably on the mode of lighting (see Kennedy, 1971, pl. 8, figs. 1, 4, 5, 8). Wright and Kennedy (1996, p. 340) have recently given their opinion that rounded subequal tubercles in the upper two rows plus feeble spiral (i.e. clavate) elongation of the tubercles in the lower two rows characterize *M. (M.) lewesiensis*. Indeed, the tubercles on the outer whorl face are coarse and globular in *M. (M.) lewesiensis* and rather granular but transversely elongated in *M. (M.) dorsetensis*, although there is no marked difference in the number of tubercles to a whorl. For us it is difficult to understand the significance of the "feeble spiral elongation of the lower tubercles". The tubercles of the lower two rows are clavate in the holotype, but the feature is not well shown in the illustration of some other specimens (e.g., Wright and Kennedy, 1996, pl. 100, figs. 23, 27).

According to Klinger and Kennedy (1978, p. 31, pl. 7, fig. F), in *M. (M.) lewesiensis* [= *M. (M.) dorsetensis* in their paper] ribs are absent or only a few traces are discernible on the lower whorl face, although they did not give a photograph of the basal view.

On the lower whorl face of the holotype ribs are extended very faintly from the tubercles of the fourth row (T.M.'s observation at the Natural History Museum, London). This character is also shown on some examples of *M. (M.) lewesiensis* by Atabekian (1985, p. 37, pl. 7, fig. 1, 1b; pl. 8, fig. 1, 1a), whereas ribs are distinctly developed on the lower whorl face of *M. (M.) dorsetensis* from the Kopet Dag (see Atabekian, 1985, p. 35, pl. 6, fig. 6, 6b) as well as in our specimens (e.g., Figure 1–4 of this paper). If this difference is confirmed in a sufficient number of specimens, it would become one of the reliable criteria to distinguish the two species.

So far, an undoubted example of *M. (M.) lewesiensis* is not found in the material of the Soeushinai area. The specimens which were tentatively identified with *M. lewesiensis* by A.I. (as written on the labels) are actually *M. (M.) oehlerti* (Pervinquier).

Mariella (Mariella) oehlerti (Pervinquière, 1910)

Figures 2–4

Turritiles gresslyi Boule, Lemoine and Thévenin, 1907 (*non* Pictet and Campiche, 1861), p. 57, pl. 13, fig. 2, 2a.

Turritiles oehlerti Pervinquière, 1910, p. 53, pl. 5, figs. 14–17; Collignon, 1929, p. 65, pl. 6, figs. 16, 17; Matsumoto, 1938, p. 23, pl. 2, fig. 7; Collignon, 1964, p. 15, pl. 320, figs. 1398, 1399.

Mariella (Mariella) oehlerti (Pervinquière, 1910); Förster, 1975, p. 190, pl. 7, figs. 7, 8; text-fig. 52; Atabekian, 1985, p. 30, pl. 6, figs. 4, 5; Wright and Kennedy, 1996, text-fig. 138 J,O,V.

Mariella (Mariella) oehlerti oehlerti (Pervinquière, 1910). Klinger and Kennedy, 1978, p. 31, pl. 3E; pl. 4E; pl. 6H–N; pl. 7G; pl. 8G–H; text-figs. 1A, B; 7B, D; 8G.

Mariella (Mariella) oehlerti sulcata Klinger and Kennedy, 1978, p. 33, pl. 8, fig. D; text-figs. 3E, 8H (? *non* pl. 3D; text-fig. 3D).

Holotype.—The specimen figured by Pervinquière (1910, pl. 5, fig. 16) from the Cenomanian of Aumale, Algeria (by original designation). Klinger and Kennedy's (1978, p. 31) designation of a lectotype (Pervinquière, 1910, pl. 5, fig. 15) was misleading, and Atabekian (1985, p. 30) erroneously followed them.

Material.—A large number of specimens from the Member My3 of the Soeushinai area are referable to this species. The representative ones among them are as follows: GK. H8500 (Figure 2–1) and GK. H8501 obtained by T.M. at loc. R518p5 and GS. 166 (Figure 2–7) collected by Y.K. at loc. R518pl from the East Suribachi-zawa; TKD 30086A (Figure 3–2), TDK 30086B (Figure 3–3) and TKD 30086C (Figure 2–6) obtained by A.I. from a nodule at loc. 81001 in the Suribachi-zawa; TKD 30546B (Figure 2–2) and A collected by W. Hashimoto from a nodule at loc. P2 in the River Shumarinai and provided to A.I. for study; GS. G163 (Figure 2–3) and GS. G164 (Figure 2–4) collected by Y.K. at loc. YKC060824 in the Sanjussen-zawa; GS. G165 (Figure 2–5) collected by Y.K. at loc. YKC050610 in the Bishamon-zawa; GS. G167 (Figure 3–1) collected by Y.K. at loc. YKC591014 and also GS. G168 (Figure 4–1) and GS. G169 (Figure 4–2) collected by Y.K. at loc. YKC020619 in the Kyoei-Sakin-zawa.

Description.—Although completely preserved specimens are hard to come by larger examples are approximately estimated at 250 mm in total whorl height and 70 mm in diameter of the last whorl. Several specimens which preserve the rostrum suggest a size dimorphism. The above larger ones, as represented by GS. G168 (Figure 4–1), may represent a macroconch, whereas GS. G167 (Figure 3–1) and TKD 30086A, B (Figure 3–2, 3) may be microconchs, for they are half of the macroconch in size. The rostrate peristome of a larger form, exemplified by GS. G169 (Figure 4–2), is twice as large as that of a smaller form, e.g., TKD 30086C (Figure 2–6).

The apical angle is low but seems to be somewhat variable between individuals and probably also with growth. On account of incomplete preservation, the actual angle is hard to measure with precision. It is roughly estimated at 25° (±5°) on the average.

The whorl is asymmetrically subquadrate to broadly rhomboidal in section. Its upper flank [i.e. upper part of the

exposed whorl face] slopes down, forming an obtusely angular (costal) or a subrounded (intercostal) shoulder at the first row of tubercles; its middle flank [i.e., main part of the exposed whorl face] is nearly vertical and forms an obtuse shoulder at the second row of tubercles with the narrow, lower flank which inclines steeply inward; the whorl junction is thus fairly deep and crenulated. The aperture is suboval and provided with a rostrum that extends at first downward and then recurves obliquely upward (see Figures 3–3; 2–6; 4–1, 2).

The tubercles are moderate in strength and coarseness; those of the first row are more prominent than others and extend upward to the ribs on the upper flank. Those of the three rows on the exposed whorl face are nearly equidistant, arranged more or less obliquely and sometimes connected by blunt riblets; those of the third row may be granular or sometimes rather clavate (i.e. extended spirally); the interspace between the second and third rows of tubercles is sometimes narrower than that between the first and second rows and, furthermore, it may be grooved to various depths (see Figure 2–5). The tubercles of the fourth row are close to those of the third row in some specimens but they are disposed along the outer margin of the basal part of the whorl. The tubercles of each row in our sample normally number from 20 to 28 to a whorl. TKD 30546B (Figure 2–2) may exemplify an extreme case (30 to a whorl), but it is referred to this species in consideration of other characters.

Aside from the bullate extension to the ribs, the tubercles of the upper two rows are conical with a rounded base. In some cases they may preserve a sharply pointed summit, but so far a highly extended spine has not been observed in our material.

Near the apertural margin the tubercles are obliquely bullate and extended to gently flexuous narrow ribs. The last rib goes on to form a blunt ridge on the rostrum, whereas the other side of the rostrum is ornamented by very fine and delicate riblets and dots (see Figures 2–6a, b, 4).

The septal suture is not well traced in our material, because the internal mould is not well exposed. It was illustrated by Förster (1975, fig. 52) on a young example from Mozambique and partly by Klinger and Kennedy (1978, fig. 1A, B) on middle-aged specimens from South Africa.

Comparison and discussion.—As the types originally described by Pervinquière (1910) and also the specimens dealt with by subsequent authors up to 1975 are so small it was difficult for us to understand the diagnosis of this species.

Based on a great number of specimens from the Lower Cenomanian of South Africa, Klinger and Kennedy (1978) have clarified the diagnosis of this species and also its relations with or distinctions from other species. Wright and Kennedy (1996, text-fig. 138 J,O,V) have finely reillustrated Pervinquière's holotype and paratypes. These two works have enlightened us in getting a proper conception of *M. (M.) oehlerti*.

In our material there are specimens which closely conform with the holotype. GK. H8500 (Figure 2–1) is such an example. They are, however, immature. The full-grown adult shell has a rostrate aperture. The three specimens illustrated in Figure 3 exemplify the adult shells of moderate size,

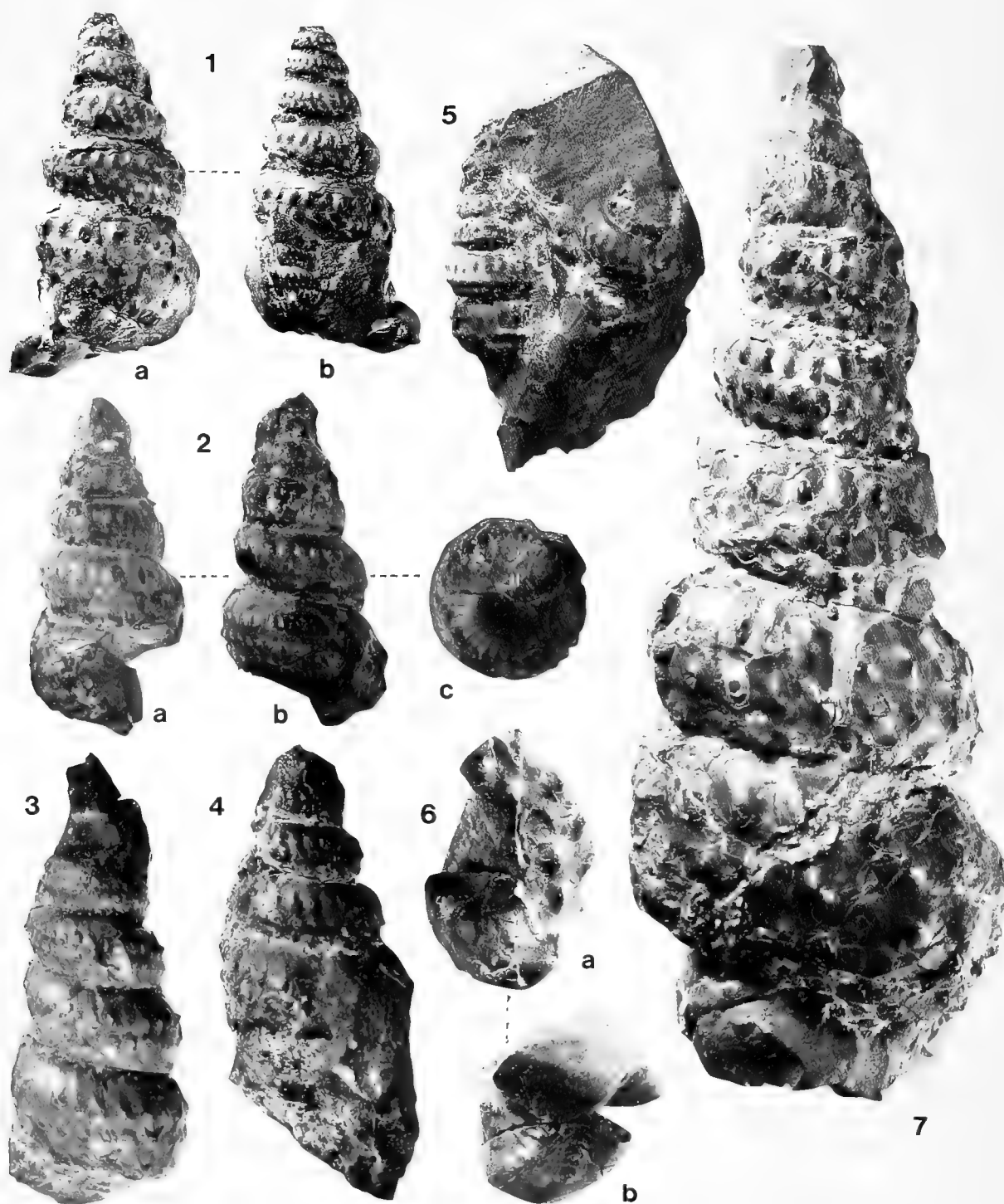


Figure 2. *Mariella (Mariella) oehlerti* (Pervinquier). **1a, b.** GK. H8500, two lateral views, $\times 1.2$ (The terminal protuberance is not a rostrum but an attached juvenile of *Anagaudryceras* sp.). **2a–c.** TKD 30546B, two lateral and basal views, $\times 1.5$. **3.** GS. G163, $\times 1.5$. **4.** GS. G164, $\times 4/3$. **5.** GS. G165, $\times 4/3$. **6a, b.** TKD 30086c, detached rostrum, external and the other sides, $\times 1$. **7.** GS. G166, a large but incomplete example, $\times 1$.

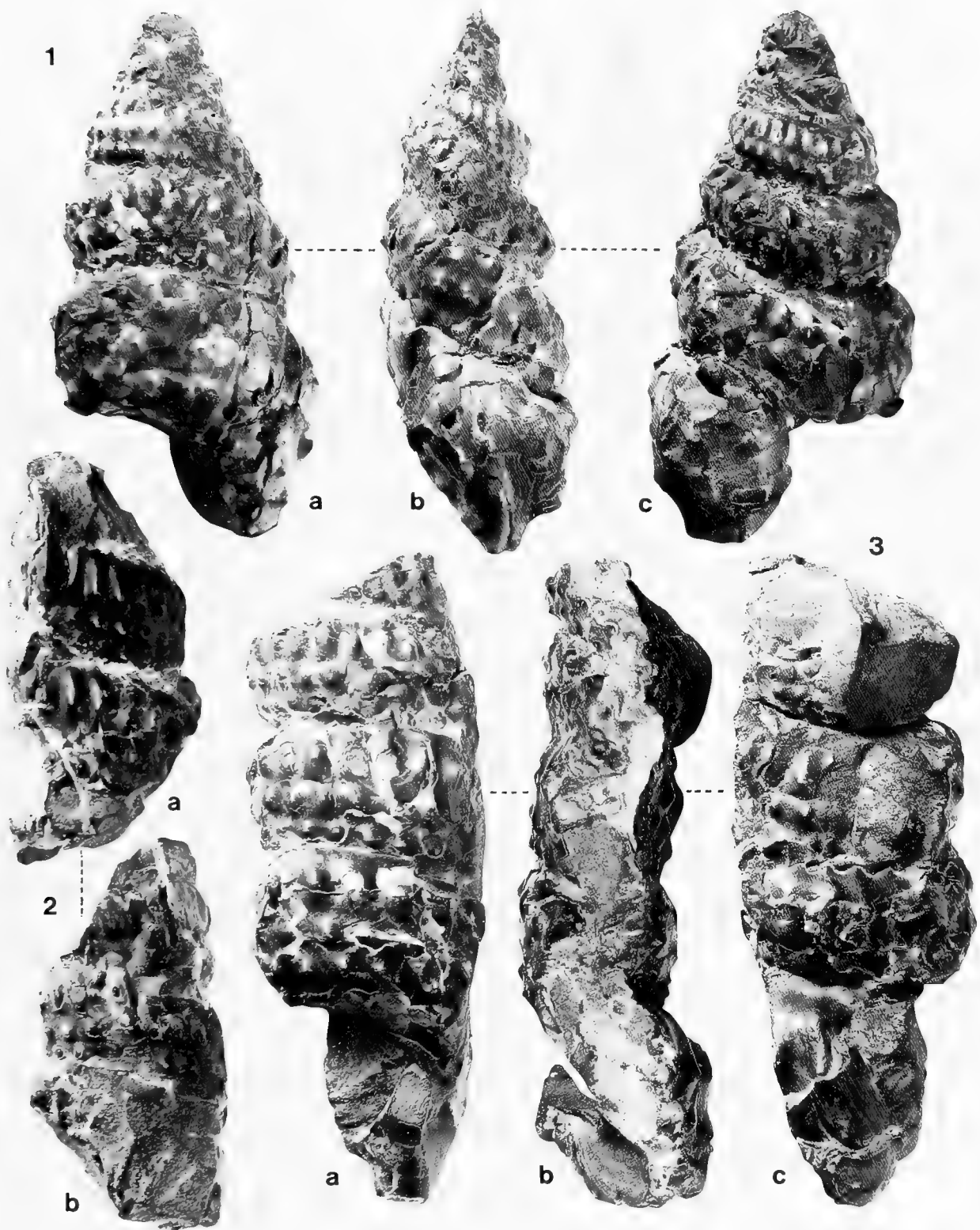


Figure 3. *Mariella* (*Mariella*) *oehlerti* (Pervinquière). More or less deformed examples of a smaller form with a rostrate peristome, all $\times 1$. **1a-c.** GS. G167, three lateral views. **2a, b.** TKD 30086A, two lateral views. **3a-c.** TKD 30086B, three lateral views.

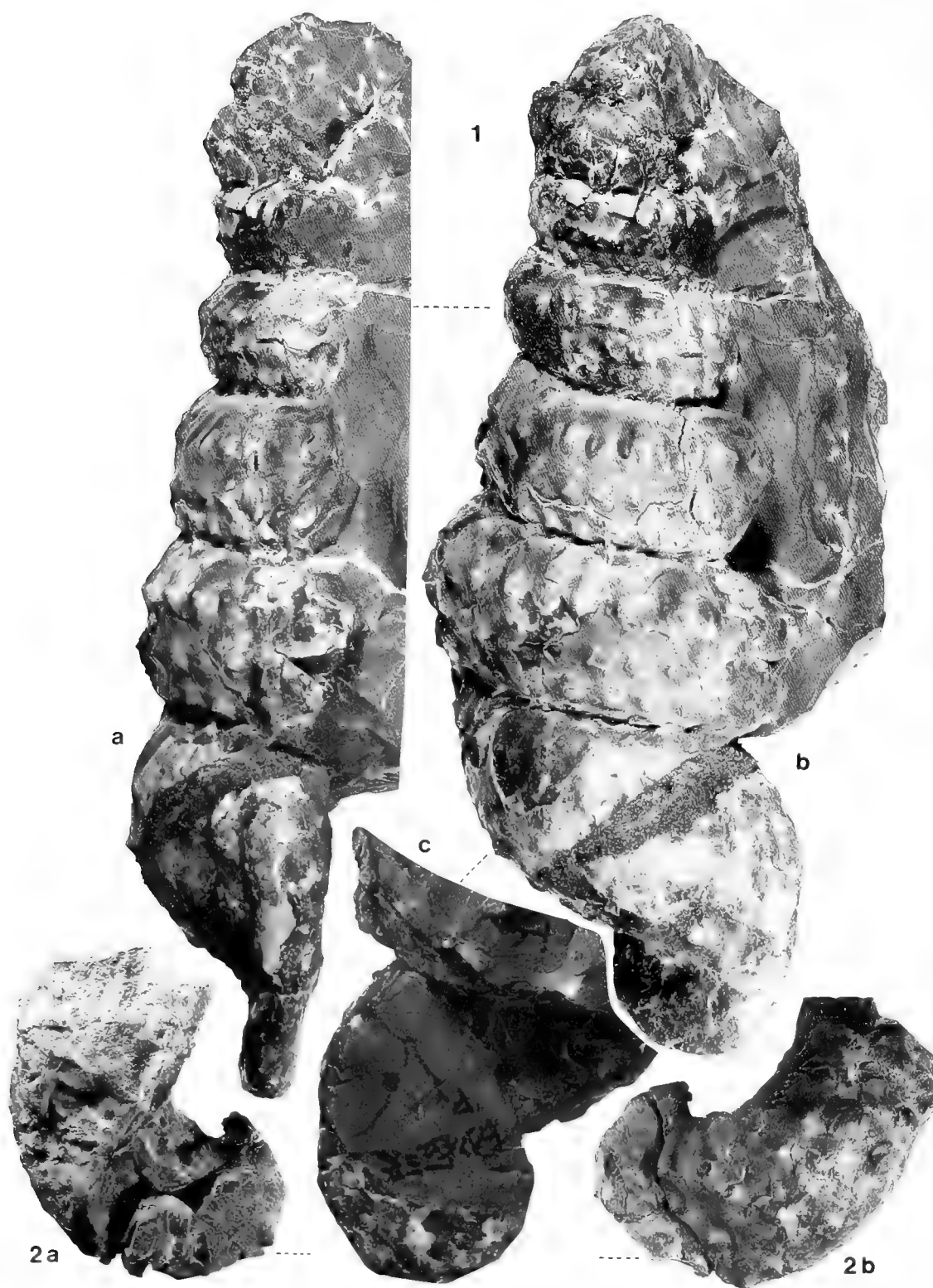


Figure 4. *Mariella* (*Mariella*) *oehlerti* (Pervinquière). Examples of a larger form, $\times 0.9$. **1a-c.** GS. G168, two lateral views (a, b) and aperture (c). **2a, b.** GS. G169, two views of a detached rostrum.

although they are considerably affected by secondary deformation. Among a number of South African specimens, BMNH C79806 (Klinger and Kennedy, 1978, pl. 6, fig. K) is an illustrated example of the adult stage. It is similar in size to our examples mentioned above, but it preserves only two whorls of the late growth stage.

In our material from the Member My3 there are much larger adult specimens which preserve the rostrate oral part. GS. G168 (Figure 4-1) is an example of such a large form. It is nearly twice as large as the specimens mentioned above. GS. G166 (Figure 2-7) is referable to a similarly large form, although its later part is not preserved. GS. G169 (Figure 4-2) is a detached piece of a rostrate oral part. It is nearly twice as large as TKD30086C (Figure 2-6), which is a detached oral part of a smaller form.

The facts described above suggest the existence of a dimorphic pair in this species. To confirm the dimorphism, it is necessary to get further evidence from the materials of other regions. Although "several hundred specimens" of this species from South Africa have been treated by Klinger and Kennedy (1978, p. 32), they did not make mention of the size variation or dimorphism. The specimens figured by them are more or less incomplete, consisting of a few whorls. The largest example among them is BMNH C79860 (*op. cit.*, pl. 8, fig. H). [Note that figure is actually $\times 5/4$, although it was indicated as $\times 1$.] It could be comparable with a part of the large specimen (GS. G168, Figure 4-1) from Hokkaido, but it lacks the oral end. On the other hand, a specimen from South Africa (*op. cit.*, pl. 6, fig. K) which possesses an incomplete rostrum is comparable with the smaller form from Hokkaido.

Dimorphism in the Turrillitidae has been noted by Wright and Kennedy (1996, p. 349) for *Turrillites scheuchzerianus* Bosc and certain other species, but Lehmann (1998, p. 37) has given comments and suggested that the observed difference might simply be size variation. There could be, however, size variation in both microconch and macroconch. For a final conclusion one should examine a sufficient number of samples.

There is another problem to be discussed. Some specimens of *M. (M.) oehlerti* from the Member My3 of the Soeushinai area show a spiral sulcus between the second and third rows of tubercles. In such cases, the tubercles rest on low ridges and may be obliquely clavate. The groove is thus variable in its degree of distinctness among the specimens and the sulcate specimens often occur together with normal ones. This feature is similar to that already noticed in the material of South Africa. Klinger and Kennedy (1978, p. 33, pl. 3, fig. D; pl. 8, fig. D; text-figs. 3D, D; 8H) have established a subspecies *M. (M.) oehlerti sulcata*. One of us (T.M.) examined some of the specimens labelled as "*M. (M.) oehlerti sulcata*", such as BM. C79952 (*op. cit.*, pl. 8, fig. D), C79951, C79950 and C79949. They seem to show a gradual change in morphology from "*M. (M.) oehlerti oehlerti*" to "*M. (M.) oehlerti sulcata*."

The holotype of the subspecies *M. (M.) oehlerti sulcata* Klinger and Kennedy, 1978 is SAS A2908. Although we have yet no opportunity to examine the actual specimen itself, its fine illustration (*op. cit.*, pl. 3, fig. D) gives us a strong

impression that it resembles a form of *Mesoturrillites aumalensis* (Coquand) such as was figured by Pervinquière (1910, pl. 14, fig. 22) (see Wright and Kennedy, 1996, text-fig. 138 S-T). Furthermore, we see that the specimen in question (SAS A2908) is similar to, if not identical with, *Mariella (Mariella) bicarinata* (Kner, 1852) (see Atabekian, 1985, p. 40, pl. 8, figs. 2-9; pl. 9, figs. 1, 2; Wright and Kennedy, 1996, p. 335, pl. 98, figs. 7, 12; pl. 102, fig. 11). We are thus, inclined to consider that it would be better to exclude the holotype of *M. (M.) oehlerti sulcata* from *M. (M.) oehlerti*. Incidentally, the above observation may be favourable to the suggestion of Wright and Kennedy (1996, p. 346) to seek the origin of *Mesoturrillites* in *M. (M.) bicarinata*.

Occurrence.—As for material. In addition, incompletely preserved specimens which can be called *M. (M.) cf. oehlerti* are found commonly in the Member My3 of the Soeushinai area. At least some of the specimens, including GK. H8500 and H8501, occur in the lower part of the Member My3 together with *Graysonites adkinsi* Young.

Records of this species from other areas in Hokkaido are so far poor, except for a fine specimen MCM A517 collected by Reishi Takashima and Koji Hasegawa from the Oyubari area. This is to be reported in detail on another occasion.

Outside of Hokkaido in Japan a few small specimens of this species were described by Matsumoto (1938, p. 23, pl. 2, fig. 7) from the Unit IIe of the mid-Cretaceous Goshonoura Group of Kyushu; *Graysonites cf. fountaini* Young occurs in the same unit (Matsumoto, 1960, p. 44, pl. 6, fig. 1; pl. 7, figs. 1-4; text-figs. 1-7, with Matsumoto *et al.*, 1960, p. 51).

M. (M.) oehlerti has been reported from the Lower Cenomanian of Algeria, Madagascar, Mozambique, South Africa and Turkmenistan (Kopet Dag) (see references in the synonymy list). The record of its occurrence in the Gulf Coast (Texas and Mexico) (Young and Powell, 1978, pl. 8, figs. 4, 6) is not clear. As species of *Graysonites* occur there, undoubted example of *M. (M.) oehlerti* should be searched for.

Mariella (Mariella) pacifica sp. nov.

Figure 5

Material.—Holotype is GS. G170 (Figure 5-1) from a nodule contained in the siltstone of the middle part of the Member My3, collected by Y.K. and N. Egashira at loc. R905 of the Hotei-zawa, a branch stream of the River Shumarinai, Soeushinai area (see Figure 7 in the Appendix).

In the same nodule as that of the holotype there are ten specimens, of which registered paratypes are GS. G171 (Figure 5-2), GS. G172 (Figure 5-3), GS. G173 (Figure 5-4), GS. G174 (Figure 5-5), GS. G175 (without figure), GS. G176-G177 (Figure 5-6), GS. G178 (Figure 5-7) and GS. G179 (without figure). Unregistered specimens are recorded from R906, at a slightly higher horizon than R905.

TKD30558 (Figure 5-8) and TKD30559 (Figure 5-12) from a nodule at loc. P4 and TKD30561A, B (Figure 5-9, 10) from a nodule at loc. P2, all taken by W. Hashimoto and transferred to A.I. for study, are probably derived from the Member My3 exposed along the middle course of the River Shumarinai.

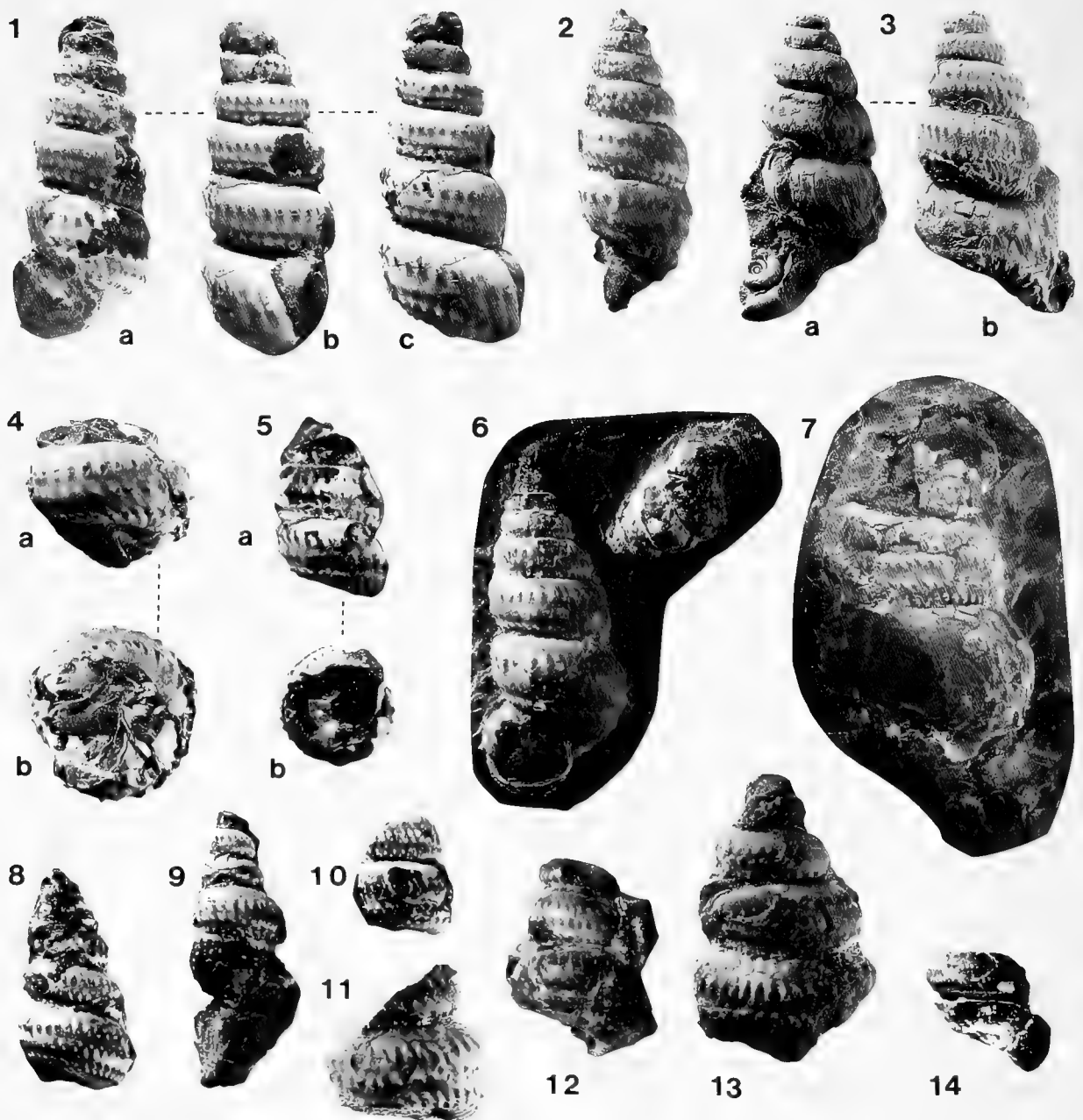


Figure 5. *Mariella (Mariella) pacifica* sp. nov. **1a-c.** Holotype, GS. G170, three lateral views, $\times 1.5$. Note that the upper whorl of the holotype is encrusted with some other organism. **2.** GS. G171, with a rostrate oral part, $\times 4/3$. **3a, b.** GS. G172, with a rostrate oral part where a juvenile *Anagaudryceras* sp. is attached, $\times 1.5$. **4a, b.** GS. G173, lateral and basal views, $\times 2$. **5a, b.** GS. G174, lateral and basal views, $\times 1.5$. **6.** GS. G176 and G177 (obliquely embedded), $\times 1.5$. **7.** GS. G178, deformed larger form with a rostrate oral part, $\times 4/3$. **8.** TKD 30558, $\times 1.5$. **9.** TKD 30561A, $\times 1.5$. **10.** TKD 30561B, $\times 1.5$. **11.** GK. H8503, $\times 2$. **12.** TKD 30559, $\times 2$. **13.** GK. H8502, $\times 2$. **14.** TKD 30560, $\times 2$. TKD 30560 is tentatively called *Mariella (Mariella)* aff. *pacifica*.

GK. H8502 (Figure 5-13) and GK. H8503 (Figure 5-11) obtained by T.M. at loc. R518 p5 of the lower part of the Member My3 in the East Suribachi-zawa, are probably referable to this species, although they are incompletely

preserved.

Diagnosis.—Small, sinistrally coiled and slenderly shaped *M. (Mariella)*, ornamented densely by numerous, small tubercles and delicate riblets in four rows at unequal intervals,

Table 1. Measurements of *Mariella* (*M.*) *pacifica*.

| Specimen Whorl | GS. C170 (holotype) | | | | G171 | | G172 |
|----------------|---------------------|------|------|-----|------|------|------|
| | 1° | 2° | 3° | 4° | 2° | 3° | 3° |
| Diameter | 15.2 | 13.0 | 11.2 | 9.3 | 13.0 | 10.8 | 12.8 |
| Height | 9.6 | 7.5 | 5.7 | 4.3 | 7.0 | 4.6 | 6.2 |
| H./D. | .63 | .58 | .51 | .46 | .54 | .43 | .48 |
| Ribs | 32 | 33 | 33 | 31 | 32 | 33 | 32 |

Height means the distance between the upper and lower seams at the adoral end of the measured whorl. Ribes mean the number of ribs or tubercles per whorl. 1°, 2°, indicate the first, second, whorls in ascending order from the bottom. Note that an undeformed whorl is selected for the measurements. Linear dimensions are in mm.

with the interspace between the first and second rows at about the mid-flank. Ribs extend upward from the tubercles of the first row; often the tubercles of the second and third rows closely but obliquely disposed, forming weak spiral ridges with a narrow groove in between; the extended fine riblets recurved on the basal surface by way of the fourth tubercles.

Description.—The shell is small and slender; its apical angle is apparently low (less than 30°); junction of whorls rather shallow; whorl section suboval to subrhomboidal, with outward sloping and gently convex upper portion of flank, nearly flat or slightly convex main part of flank, and narrow and inward-sloping lower portion. Obtuse shoulders may thus be formed at the upper and lower edges of the main part of flank. Basal surface of the whorl is gently convex, sloping to a narrow umbilicus.

Ornament consists of numerous, densely set, fine tubercles and extended delicate riblets, numbering about 30 to 40 to a whorl in each row. The tubercles are normally in four rows at unequal intervals; the first row slightly above the mid-flank, the second somewhat below the mid-flank, the third close to the second and the fourth along the lower whorl seam on the outer margin of the basal surface, where riblets are recurved. The tubercles are of unequal intensity between the rows; those of the first row are slightly coarser than others and extend upward to short ribs; those of the second and third rows are finer, somewhat oblique and disposed en echelon; often they appear to form blunt spiral ridges with a sulcus in between. The tubercles of the fourth row are very fine and close to those of the third row; occasionally the fourth-row tubercles are scarcely discernible or undeveloped.

Near the apertural margin ribs become flexuous and continuous, connecting transversely elongates tubercles (see GS. G171, G172 and G178; Figure 5-2, 3, 7). Regrettably, the recurved part of the rostrum is not preserved. At any rate, the above three specimens represent the adult shell. The holotype (GS. G170) is also nearly adult. The three specimens, GS. G170, G171 and G172 (Figure 5-1-3) are equally small, with total whorl heights about 40 mm and diameters of last whorl 15 mm or so. On the other hand GS. G178 (Figure 5-7) is somewhat larger, although it is deformed and lacks earlier whorls. Again dimorphism can be considered, if not definitely concluded.

Measurements.—See Table 1.

Comparison.—In respect of a small and slender shell with

numerous, fine and delicate tubercles and riblets, this species may be closely allied to *M. (M.) numida* (Pervinquière) (1910, p. 53, pl. 5, figs. 12, 13), from the Cenomanian of Algeria, but the holotype of that species (refigured by Wright and Kennedy, 1996, text-fig. 138L) is dextral and seems to possess a lower apical angle (about 18°) and four rows of tubercles wholly exposed on the outer face of a whorl. For the exact comparison more specimens including an adult example of *M. (M.) numida* are required.

In having numerous tubercles and obliquely extended riblets, *M. (M.) pacifica* is apparently similar to *M. (M.) torquatus* Wright and Kennedy, 1996 (p. 334, pl. 100, figs. 2, 20, 21), from the Lower Cenomanian of England. In the latter the rows of closely set tubercles form distinct spiral ridges. In the former the tubercles are normally not so much crowded and the ridges are weaker. TKD30560 (Figure 5-14) from loc. P1 is exceptional in that its tubercles and riblets are so crowded and numerous (about 50 to a whorl) that the rows of tubercles form fairly distinct spiral ridges. There is, however, some extent of variation in the distinctness of the ridges in *M. (M.) pacifica*. For instance, TKD30559 (Figure 5-12) and TKD30558 (Figure 5-8) appear to show intermediate features. There is, thus, a certain extent of variation in the fineness of tubercles and appearance of ridges in *M. (M.) pacifica* and also in *M. (M.) torquatus* (see the three figures cited above). The undoubted difference between the two species is in the disposition of the rows of tubercles. Namely, in *M. (M.) torquatus* the first row is higher in the upper part of the whorl face and the second row is at the middle of the whorl, whereas in *M. (M.) pacifica* the interspace between the first and second rows is at the mid-flank. This is maintained even in TKD30560. There is also a difference in whorl shape between the two species; rectangular versus suboval in whorl section.

In respect of the small and slender shell, *M. (M.) pacifica* is somewhat similar to *M. (M.) camachoensis* (Böse) (1923, p. 149, pl. 10, figs. 32-37) (see also Clark, 1965, p. 43, pl. 13, figs. 6, 8; pl. 18, fig. 8), from the Upper Albian (a unit correlatable with the Pawpaw Formation) of Mexico, but the tubercles of *M. (M.) pacifica* are more numerous and disposed in rows at unequal intervals; those of the first row are coarser and extended upward to ribs.

M. (M.) pacifica resembles *M. (M.) oehlerti* (Pervinquière) (*vide supra*) in general appearance and especially in the disposition of the rows of tubercles. The former is characterized by its slender shell shape, with a shallower inter-

whorl junction, suboval instead of subquadrate to rhomboideal whorl section and on the average finer, denser and more numerous tubercles and riblets in comparison with the latter. Should the suggested dimorphism be warranted in each of the two species, the size difference at the adult stage would be distinctive.

Klinger and Kennedy (1978) found in their South African material of *M. (M.) oehlerti* large variation in the number of tubercles. The number ranges from 15 to 28 per whorl with an exceptional 30; for the majority the range is from 18 to 24. This is conformable with our material of *M. (M.) oehlerti*. In the case of *M. (M.) pacifica* under investigation, the counted range is normally from 30 to 40 per whorl. The two species are thus separable on this point, although the range is fairly wide in each of them. However, TKD30560 mentioned above (with 50 tubercles per whorl) is rather extreme and it is better to call it tentatively *M. (M.) aff. pacifica*.

With respect to numerous, densely set tubercles, *M. (M.) miliaris* (Pictet and Campiche, 1861) (p. 136; 1862, pl. 58, fig. 5) (see Renz, 1968, p. 88, pl. 18, fig. 10 for the reillustration of holotype) is somewhat similar to *M. (M.) pacifica*, but the rows of tubercles are nearly equidistant and the apical angle has been described as larger in that species. It is closely related to *M. (M.) bergeri*, as Spath (1937, p. 515) has already mentioned. *M. (M.) miliaris* normally occurs in the Upper Albian but ranges up to the Lower Cenomanian in England (see Wright and Kennedy, 1996, p. 333).

Occurrence.—As for material. The type locality is in the middle part of the Member My3. This species occurs so far in the Lower Cenomanian of Hokkaido. Its true vertical range and geographical distribution should be determined by further investigations.

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For the material of this palaeontological study we are indebted to the cooperative field work conducted by W. Hashimoto and also by T. Nishida. We have been much enlightened by the results of previous palaeontological studies, especially those by Clark (1965), Klinger and Kennedy (1978), Atabekian (1985) and Wright and Kennedy (1996), although our views may not be always agreeable with them. Naoko Egashira and Seiichi Toshimitsu helped us in photography and Kazuko Mori assisted us in preparing the manuscript.

Appendix

Locality guide for selected Cretaceous fossils of the Soeushinai area

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The localities of the Cretaceous fossils in the Soeushinai area and the lists of identified species (mainly Mollusca and Foraminifera) have been indicated in a number of route maps

and tables in the papers by Nishida *et al.* (1992, 1993, 1996, 1997, 1998a, b). These papers are written in Japanese and the maps are too numerous. Hence, two comprehensive maps (Figures 6 and 7) are presented here. They are compiled from some of the previous maps with necessary modifications. The specimens of *Mariella* species with register numbers in the descriptions and a few unregistered ones are indicated in the maps. Moreover, the maps contain localities of selected mid-Cretaceous guide species which are particularly important for interregional correlation.

The geology is outlined in the maps. A thick broken line is a fault and a dotted line is a boundary of lithostratigraphic units. The Lower Yezo and Middle Yezo Subgroups are abbreviated to Ly and My. My1, My2, My3 and so on are successive members of My; T is the Tertiary (mainly Miocene); Q is a leucocratic intrusive body. A megafossil locality is indicated by a small solid circle (in situ) or by a cross mark (fallen or transported nodule).

Notes are briefly given below in accordance with the investigated routes, of which (1)–(3) are shown in Figure 6 and (4)–(10) in Figure 7.

(1) *Main course of the River Sounnai* (part) (upstream).—R887 (a nodule derived probably from the upper part of Ly): *Hysterocheras orbigny* (Spath), *Pseudohelicoceras* sp. etc. R880 (nodules in mudstone in the upper part of My1): *Mortoniceras* (*Deiradoceras*) sp., etc. R34 (mudstone alternated with sandstone, lower part of My2): *M. (Durnovarites)* cf. *subquadratum* Spath etc. R803 (laminated mudstone and sandstone, upper part of My2): *Mariella bergeri* (Brongniart), *Mortoniceras* (*M.*) cf. *minor* Spath. R813 (ditto): *M. bergeri*, *Bhimaites kawai* Matsumoto and Egashira. The above faunules at four levels are correlated with successive zones of the Upper Albian.

(2) *East Suribachi-zawa* (E in Figure 6).—R525 (laminated mudstone in the upper part of Member My2): *Bhimaites* cf. *kawai* and *Inoceramus* n. sp. (small, nearly equivalent, finely ornamented species, probably identical with the late Albian species from Mont Risou illustrated in Gale *et al.*, 1996, figs. 21f, j; 31g). R520 (nodules derived from the basal part of My3): *Mariella* aff. *bergeri* (to be described in Part 2), *Graysonites adkinsi* Young, *Stoliczkaia* (*Lamnayella*) *sanctaecatherinae* Wright and Kennedy etc. R518 (nodules from the lower part of My3): *Mariella oehlerti*, *M. dorsetensis*, *M. cf. pacifica* etc. R515 (mudstone in the lower part of My3): *Graysonites* sp.

(3) *Suribachi-zawa* (S in Figure 6 and branch rivulets) (upstream).—R875 (a nodule derived from My3): *Mariella miliaris* (Pictet and Campiche) (to be described in Part 2). A181001 (nodule from My3) and R543 (nodules in mudstone of My3): *M. oehlerti* etc. R575 (ditto): *M. dorsetensis*, *M. oehlerti*, *Graysonites* cf. *adkinsi* (nearby derived nodule). *Inoceramus* aff. *reachensis* Etheridge. R534 (nodules in laminated sandstone and mudstone of My2): *Inoceramus* n. sp. (same as sp. at R525), *Mortoniceras* cf. *minor* etc. R433 and A181007 (nodules from My3): *M. dorsetensis*, *Stoliczkaia* (*Lamnayella*) cf. *sanctaecatherinae* etc. R438 (nodules from My3): *M. dorsetensis* etc. R471 (mudstone of My3): *Inoceramus* aff. *reachensis*. R449 (nodule from My3?): *M. cf. carrancoi* (Böse) (to be described in Part 2). R456 (nod-

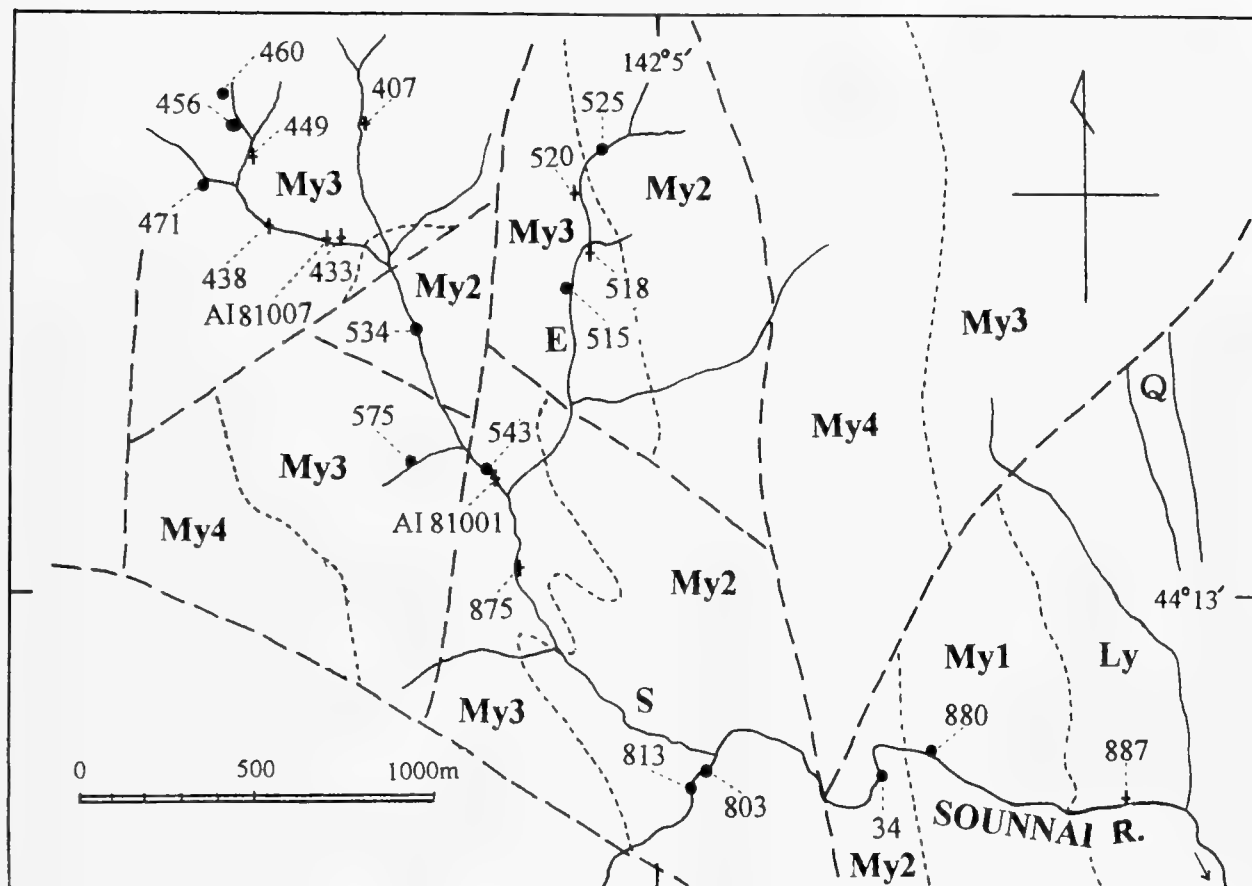


Figure 6. Route map of the Suribachi-zawa and part of the Sounnai River, showing localities of *Mariella* and selected guide species (compiled from Nishida *et al.*, 1996, figs. 3–5 and 8 and also Nishida *et al.*, 1997, figs. 1, 2). See text for the marks and abbreviations. Some of the numbered localities with prefix AI are referred to TKD specimens. Many others are concerned with the main material of this study. They should have the prefix R, which is omitted in this and the other map for brevity. Note that prefix AI is not used in the original label of TKD and in the main text of this paper.

ule in sandy siltstone of My3): *M. dorsetensis*, *Stoliczkaia* (*Lamnayella*) cf. *amanoi* Matsumoto and Inoma. R460 (nodule in mudstone of My3): *M. oehlerti*, *Graysonites* cf. *adkinsi*. R407 (nodule from My3): *M. cf. pacifica*.

(4) NW branch rivulet of the Sanjussen-zawa.—Loc. YKC060824 (nodule from My3): *M. dorsetensis*, *M. oehlerti* etc.

(5) Upper reaches of the Kyoei-Sakin-zawa.—At two localities YKC591014 and YKC020619 *Mariella oehlerti* was collected in nodules from My3. Not far from these localities *Graysonites wooldridgei* was obtained in situ at loc. YKC010618 and in a transported nodule at loc. YKC040808. Somewhat downstream from them at loc. KY768 *S. (L.) sanctaecatherinae* was obtained from a transported nodule. These localities are all in the area of My3. Still further downstream at locs. YKC060918 and KY356 *G. adkinsi* was collected from transported nodules. The two localities suggest a small outcrop of My3 within an otherwise Tertiary area.

(6) Ebisu-zawa and Hotei-zawa (EB, HT in Figure 7).

—R557 and R560 (laminated mudstone and sandstone): *Inoceramus* n. sp. (same as the one from R525). R567 (nodule from My3): *M. cf. oehlerti*. R901 (nodule from My3): *Graysonites wooldridgei*. R905 (nodule in mudstone of My3): *M. pacifica*, *M. dorsetensis* etc. R906 (ditto): *M. pacifica*, *M. gallienii* (Boule, Lemoine and Thévenin), *S. (L.) sanctaecatherinae*.

(7) Middle course of the R. Shumarinai and a branch rivulet Fukuroku-zawa (FR in Figure 7) (upstream).—R8003 (laminated mudstone and sandstone of My2): *Bhimaites kawai*, *Inoceramus* n. sp. (same at R525). AI71204 (nodule from My3): *M. dorsetensis*. KY350 [=R8054] (nodule in mudstone with sandy laminae of My3): *S. (L.) sanctaecatherinae*. AI P1, P2, P4 (nodules from My3): *M. aff. pacifica*, *M. oehlerti*, *M. pacifica*. R926 (large nodule derived from My3): *M. oehlerti* etc. R917 (nodule from My3): *M. oehlerti*. R919 (nodule in mudstone of My3): *M. oehlerti*, *Ostlingoceras* cf. *bechii* (Sharpe), *Inoceramus* aff. *reachensis* etc. R930 (nodule from My3): *M. oehlerti*, *I. aff. reachensis*. R931 (nodule from My3): *M. cf. oehlerti*.

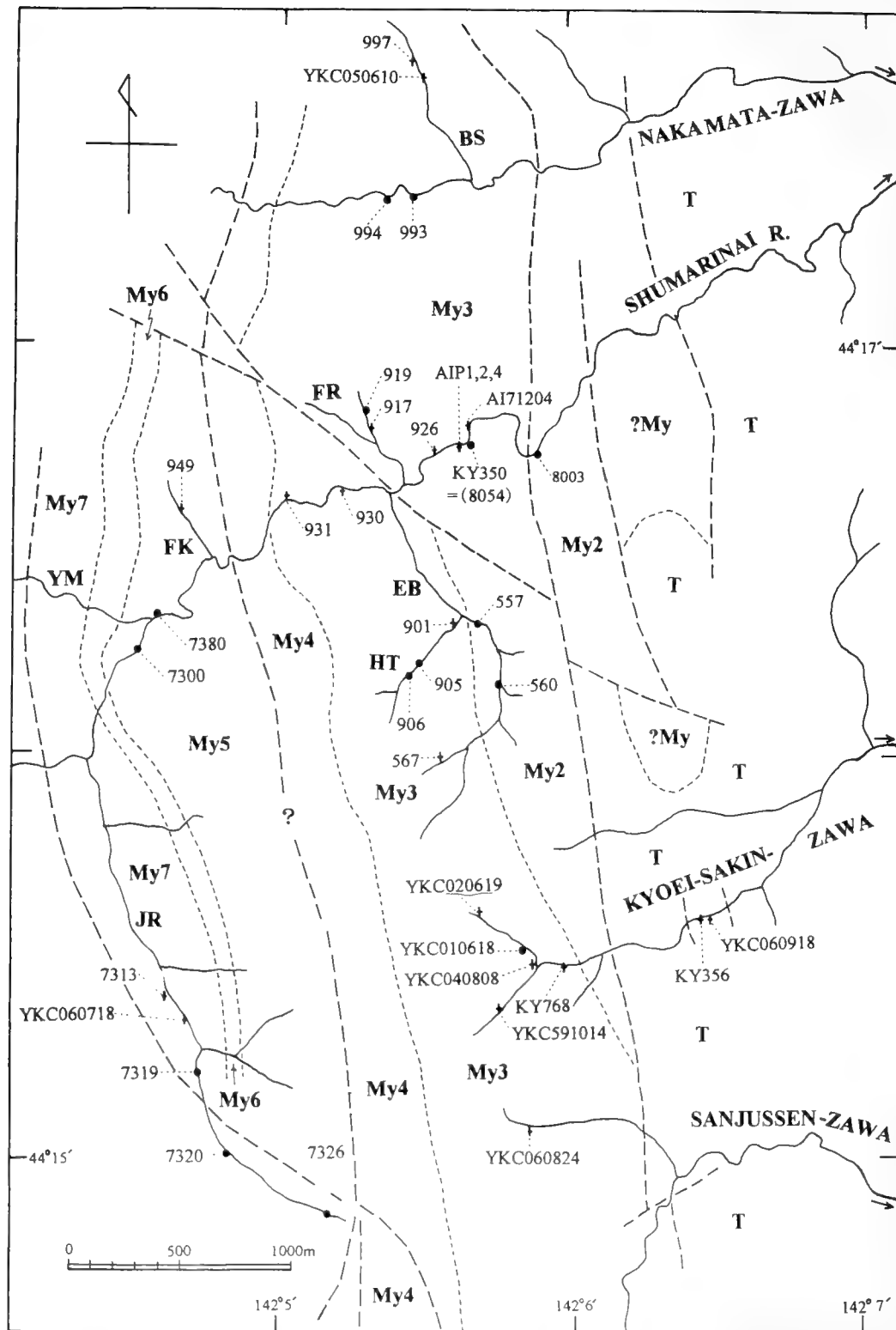


Figure 7. Route map of the area across the middle course of the Shumarinai River, showing localities of *Mariella* and selected guide species (compiled from Nishida *et al.*, 1996, fig. 7; Nishida *et al.*, 1997, figs. 7, 8; Nishida *et al.*, 1998b, figs. 2-4 and 7). See text for the marks and abbreviations. Prefix KY or YKC to a locality number refers to Katsujo Yokoi's or Y.K.'s collections by their independent field work. Other numbers are as for Figure 6.

(8) Middle course of the Nakamata-zawa and its tributary Bishamon-zawa (BS in Figure 7) (upstream).—YKC050610 (nodule derived from My3): *M. oehlerti*. R997 (nodule from My3): *S. (L.) sanctaecatherinae*. R993 (nodule in mudstone of My3): *M. oehlerti*, *M. pacifica*, *Graysonites* sp., *Zelandites* cf. *inflatus* Matsumoto. R994 (nodule in mudstone of My3): *Inoceramus* aff. *reachensis*.

(9) Upper-middle course of the R. Shumarinai and a branch rivulet Fuku-no-sawa (FK in Figure 7) (upstream).—R949 (nodule from lower part of My5): *Turrilitis acutus* Passy, *Inoceramus pictus minus* Matsumoto. R7380 (mudstone in the middle part of My5): *Inoceramus ginterensis* Pergament. R7300 (sandy mudstone in the upper part of My5): *Wellmanites japonicus* Matsumoto, Takahashi and Sanada, *Inoceramus* cf. *pennatulus* Pergament etc.

(10) Jyurou-zawa (JR in Figure 7) (upstream).—R7313 (nodule from My7): *Vascoceras durandi* (Thomas and Peron). YKC060718 (nodule from My7): *Muramotoceras yezoense* Matsumoto, *Inoceramus kamuy* Matsumoto and Asai, *Mytiloides subhercynicus* (Seitz), etc. R7319 [=YKC010625] (huge nodules in mudstone of My7): *Pteropuzosia kawashitai* Matsumoto. Based on the above species My7 is referable to the lower part of the Turonian. No species of the Turrilitidae has been found from My7. Being separated by a fault, mudstones with some beds of sandstone are exposed in the uppermost course of the Jyurou-zawa where ammonoids and inoceramids of the upper to middle Cenomanian have been collected at locs. R7320–7326, while turrilitids have yet to be searched for.

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A new crayfish Family (Decapoda : Astacida) from the Upper Jurassic of China, with a reinterpretation of other Chinese crayfish taxa

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Abstract. The highly sporadic fossil record of freshwater crayfish is improved by the discovery of several new specimens from the Upper Jurassic Jehol Group of Liaoning Province, north-east China. As a result of work on this material, the Family Cricoidoscelosidae is erected to accommodate specimens possessing highly atypical features among the Infraorder Astacidea belonging to the new genus and species *Cricoidoscelosus aethus*. Furthermore, *Astacus spinirostris* Imaizumi (1938) is synonymized with *A. lincenti* van Straelen (1928b) and is moved from the Family Astacidae to the family Cambaridae and to the new genus *Palaeocambarus*. Thus, a solution is suggested to the problematic biogeographic issue of the presence of the genus *Astacus* in a region presently occupied only by cambarid crayfish, a generic assignment that was made tentatively in the first place. In addition, new questions now arise with respect to the origins and early development of crayfish in the Asiatic region and perhaps even globally.

Key words : Astacida, China, crayfish, palaeobiogeography

Introduction

Members of the decapod Infraorder Astacidea, commonly referred to in English by the vernacular term 'crayfish', are also known by many other common names worldwide : crawfish, paper-shell crabs, ecrevisse, yabbies, mud-bugs, flusskrebs, rak, ditch bugs and koonac are just some of these names. With over 500 species currently known, which occur indigenously in tremendous numbers on all continents with the exception of Africa, this is perhaps not surprising (Adegboye, 1981 ; Hobbs, 1988 ; Pitre, 1993).

The evolutionary history of the Superfamily Astacoidea is currently the subject of some debate. The more traditional perspective, as suggested originally by Ortmann (1902, 1905), is that the crayfish as we know them today originated in a benthic marine environment similar to that occupied by the marine lobsters. From this ancestral stock emerged three major lines : the extinct Erymidae ; the relatively conservative Nephropidae (ancestors of the modern true lobsters) ; and the highly varied and widely dispersed Astacoidea and Parastacoidea, the 'true crayfishes', which then moved into the freshwaters of Laurasia and Gondwana as the result of two separate invasions.

A more recent perspective, however, is that of Scholtz

(1995) and Scholtz and Richter (1995), in which the freshwater crayfishes are more closely related to the Thalassinida and Meiura (Brachyura and Anomala) than to the Homarida (forming a monophyletic group they refer to as the Fractosternalia). They suggested that the worldwide distribution of freshwater crayfish is the result of a single invasion into freshwater during the Triassic onto the 'supercontinent' Pangaea, which then diversified into the groups Parastacoidea (in Gondwana) and Astacoidea (in Laurasia) with the Late Mesozoic break-up of Pangaea.

Despite their relatively long geologic history, the fossil record for the crayfish is not very well understood. Many of the recent references to fossil crayfish originate from the research group of Rodney Feldmann, including the description of new taxa and/or redescription of previously described taxa (Feldmann, 1994 ; Feldmann *et al.*, 1981) as well as such oddities as evidence of crayfish predation (Feldmann and May, 1991). Other sources of information on the palaeontological record for the Astacida include Rathbun (1926), van Straelen (1928a), Albrecht (1982, 1983) and Cope (1871). Much work has been done with respect to the global distribution patterns of the living Astacidea (e.g., Hobbs, 1988 ; Huxley, 1884 ; Ortmann, 1902), stemming largely from their wide use as an aquaculture crop ; however, relatively

little has been done with respect to a comprehensive analysis of the fossil members of this group beyond strict taxonomy.

Among the more intriguing of fossil astacids has been material from the Late Mesozoic of China. We will here build on the original works of van Straelen (1928b) and Imaizumi (1938) and their respective description of two species of fossil freshwater crayfish, *Astacus licenti* and *A. spinirostris*, from the Upper Jurassic (Jehol Group) of Liaoning Province, north-east China. This reassessment is prompted by the discovery of several new, well-preserved specimens from the region.

Collection localities

New material described in this paper was obtained from outcrops in Dawangzhangzi and Daxinfazi villages, Ling-yuan County, Liaoning Province, probably belonging to the Yixian Formation of the Upper Jurassic Jehol Group (Figure 1). While the general collection regions are known, their actual locations are vague because local farmers, who sell the specimens they collect to visiting academics, refuse to

reveal their exact locations (one of which has actually been buried by the Chinese government to avoid poaching!). Enough is known of the geology of the region, however, to allow determination of the formations from which they have been collected.

Systematic Paleontology

Order Decapoda
 Infraorder Astacida
 Superfamily Astacoidea
 Family Cambaridae
 Subfamily Cambarinae
 Genus *Palaeocambarus* gen. nov.

Type species.—*Astacus licenti* van Straelen, 1928b

Diagnosis.—Entire dorsal surface of cuticle covered with fine granulations. Rostrum with basal lateral spines. Elongate, bladelike scaphocerite. Chela of first pereiopod long and narrow with extensive pitting and spination. No hooks visible on ischia. Pleura large and rounded on abdominal segments 2–5, 2nd pleuron being largest. Pleopods elongate.

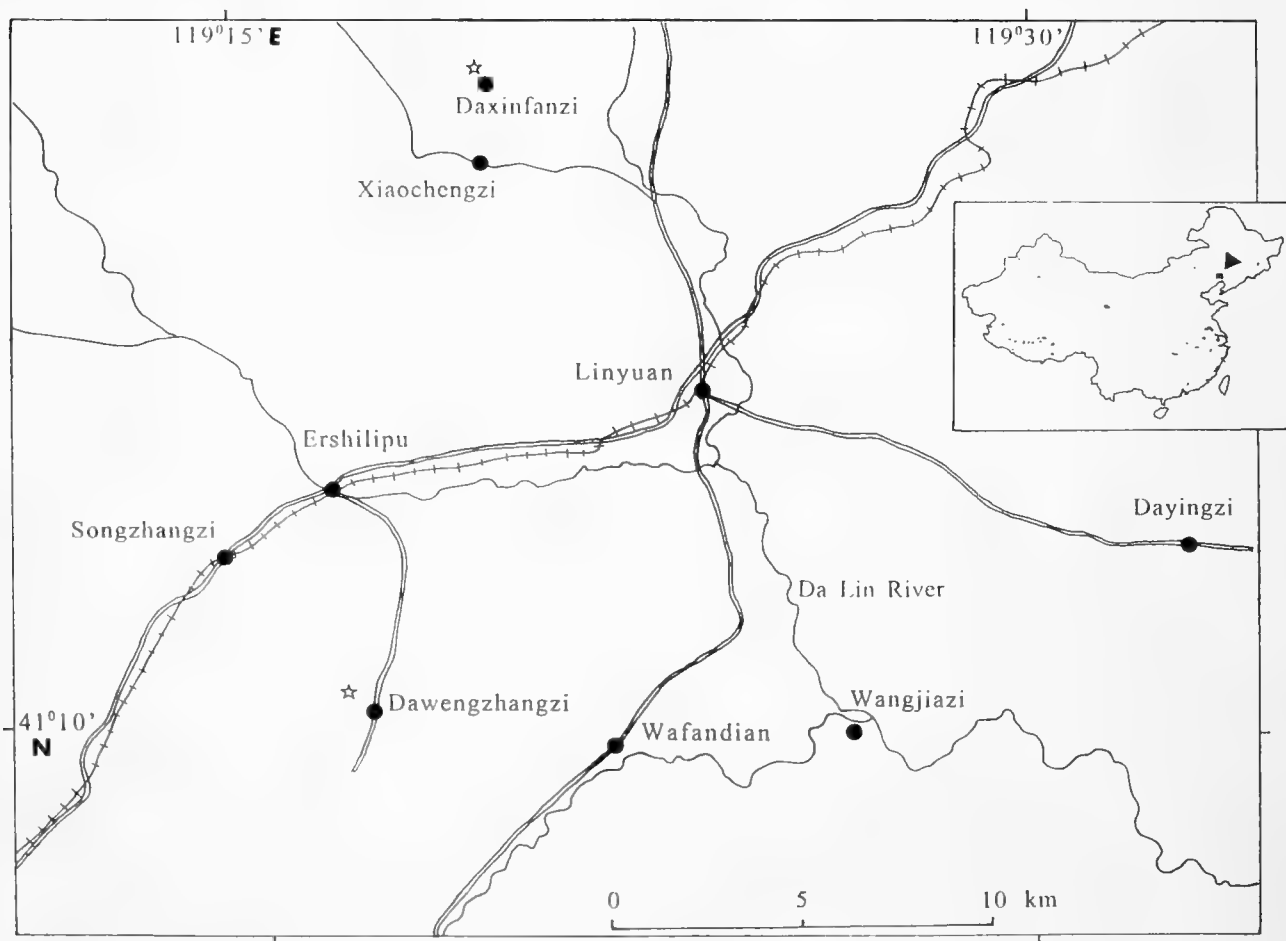


Figure 1. Locality map showing fossil crayfish collection localities near Daxinfanzi and Dawengzhangzi (stars).

gate and blade-like, with no specialization on first. Telson subrectangular with pair of large lateral spines and rounded distal margin.

Etymology.—The name of the genus is formed from 'palaeo', meaning 'ancient', in combination with 'Cambarus', reflecting the new placement of its sole retained species in the Family Cambaridae.

***Palaeocambarus licenti* (van Straelen), 1928b**

Figures 2, 4–6

Astacus licenti Van Straelen, 1928b, p. 133–135, figs. 1, 2; Imaizumi, 1938, p. 176, pl. 23, figs. 1, 2, 4, 5, 6, 11; Hamada and Itoigawa, 1983, p. 74, Pl. 3, fig. 6; Hobbs, 1988, p. 73.

Astacus spinirostris Imaizumi, 1938, p. 176–177, pl. 23, figs. 9, 10, 12, 13, pl. 22, fig. 1; Hobbs, 1988, p. 73.

Diagnosis.—As for genus.

Emendation to Description.—Rostrum elongate and triangular with smooth margins. Approximately twice as long as wide at base (largest observed being 15 mm long and 7 mm wide at base). Length roughly one-third that of cephalothorax. A pair of anteriorly directed spines near base of rostrum that extend to approximately one-third rostrum's length (NIGP 126338). One specimen (NIGP 126342) shows two rows of small tubercles on ventral surface of rostrum. A single specimen (NIGP 126338) possesses small mid-dorsal spine at base of rostrum (Figures 4b, 4c).

Carapace developed, covers thorax completely. It extends partially over first pleomere mid-dorsally and completely so laterally due to slight postero-lateral enlargement (Figures 5a, 6a); simply decorated, possessing only a sinusoidal cervical groove (concave medially, curved convexly mid-laterally, concave again at lateral carapace margin) as well as a pair of short branchiocardic grooves that extend posteriorly from medial cervical groove (NIGP 126353, 126338: Figure 4c). A single specimen (NIGP 126338) possesses a pair of well-developed gastric spines (Figure 4c). A slight ridge along lateral and posterior edges, but not evident along anterior margin. Optic notch well developed; adjacent anterolateral margin gently rounded (Figure 6a). Entire carapace surface with granulated texture, several small spines/protrusions situated near cervical groove and around anterolateral region of carapace (NIGP 126338, 126353).

Antennules biflagellate, with medial flagellum larger than lateral flagellum. Peduncle not fully preserved on any specimens, although several specimens possess some peduncular segments. NIGP 126338 shows distal segment only, which is subrectangular in shape, slightly longer than wide, has rounded edges and is very small (less than 1 cm²). NIGP 126346 with two distalmost segments, in shape with rounded edges and similar size dimensions. Middle segment noticeably more square than distalmost segment but equal in size. Distalmost segment similar in shape to others mentioned but with slight anterior projection on outer margin, possibly remains of small spine. Second segment approximately twice as wide as distal segment, suggesting it may be portion of basal segment, which is typically considerably

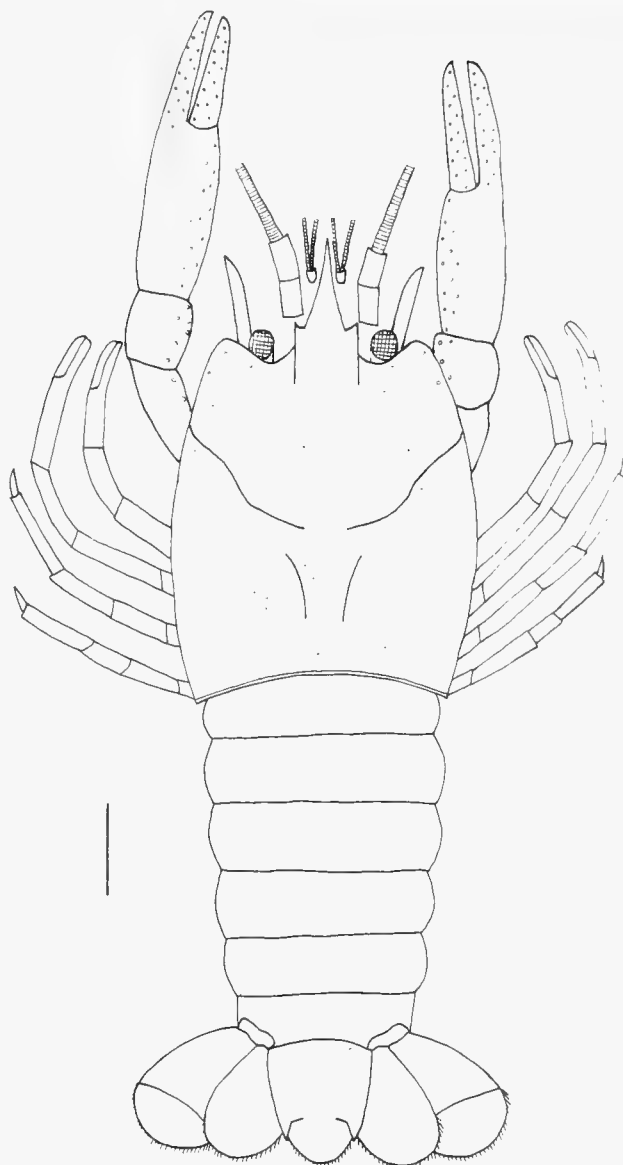


Figure 2. A reconstruction of *Palaeocambarus licenti* in dorsal view. Scale bar equals 1 cm.

larger than the other two antennular peduncle segments in recent crayfish. Antennular flagellae exceed 10 cm in length (Figures 4b, c, 5a, 6a).

Antennae each possess a single flagellum that is considerably longer than those of antennules (NIGP 126339 possesses a flagellum ~60 mm long, almost equal to total body length). Distal segments of peduncle relatively clear, but proximal peduncle arrangement difficult to interpret due to their frequently being overlapped by other structures such as antennal scales or rostrum. Distalmost segment rectangular in shape with concave proximal margin, long axis along length of antennae, and shows dimensions of approximately 3 mm width by 4 mm length. Adjacent segment similar in

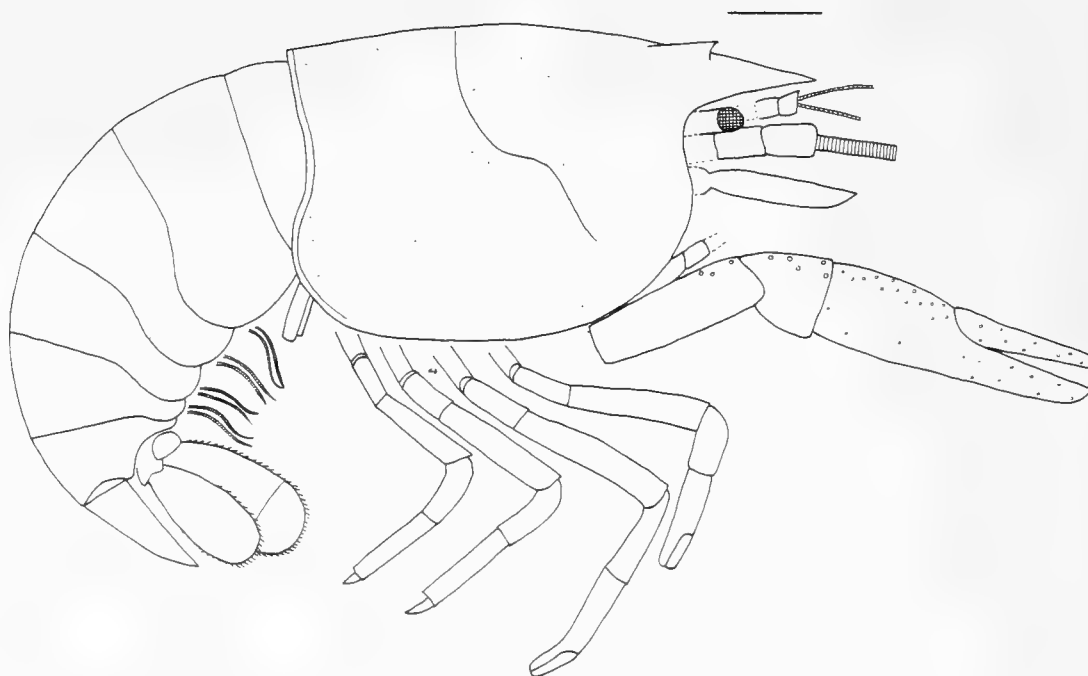


Figure 3. A reconstruction of *Cricoidoscelosus aethus* in lateral view. Scale bar equals 1 cm.

shape and size but lacks curved proximal edge. Middle segment rectangular in shape and similar in length to two distalmost segments, approximately 2/3 as wide as long; attached laterally to basis, which is short (approximately 2 mm) and wide (4 mm) and possesses an arcuate proximal margin. Coxa rectangular in shape with slightly convexly curved posterior margin, slightly less wide than basis and possesses medial anterior projection, which 'fills' the posterior groove in basis (NIGP 126338; Figures 4c, 6a).

Well-developed, blade-shaped scaphocerites extend from lateral half of each antennal basis. They reach maximum length of 15 mm, are setose along lateral margins (only setal bases, not setae themselves, preserved). One specimen (NIGP 126343) possesses small, medially directed process at anterior end of scaphocerite (Figures 4a, 4c, 5a, 6a).

Eyes located near base of scaphocerites, always somewhat deformed but were probably round or slightly ovoid and approximately 2 mm wide. They were probably closely associated with body, with short eyestalks of 1–2 mm, are always found superimposed over rostrum and/or antennal peduncle (i.e., NIGP 126342).

Prominent epistome, close to 10 mm in width, visible on ventrally preserved specimens suggesting it was heavily sclerotized in life (as seen with recent crayfish). It possesses an arched v-like shape and is directed anteriorly. Medial process present near the anterior end, with two small longitudinally arranged pits. Anteriormost end possesses forward-directed process, approximately one-quarter width of labrum and trapezoidal in shape, wider edge anteriormost (NIGP 126342; Figure 6c).

Some dorsoventrally oriented specimens show details of

well-developed gastric mill, triangular in shape, directed posteriorly and found immediately behind labrum (NIGP 126342); made up of two sets of very small, serially arranged peg-like teeth in slightly inwardly curved rows, approximately 16 teeth per element. No median tooth present. Moulds of paired circular gastroliths, up to 7 mm in width, prominent in several specimens: in NIGP 126338 and 126353, one has rounded convex surface while other possesses an outer depressed ridge with raised circular region (Figures 4c, 5a, 6c).

Elements of first and second maxillipedes preserved on some specimens; however, they are impossible to interpret with any certainty due to being damaged and/or obscured by anterior structures such as carapace, 3rd maxillipede and 1st thoracomere. Third maxillipede possesses large ischium, up to 10 mm in length and 3 mm in width. Extensive crista dentata found along ischial inner margin. Merus is small, approximately 2 mm long and 4 mm wide and ovoid in shape. Carpus slightly less in width than merus and is rectangular in shape. Propodus rectangular in shape and approximately 2 mm by 4 mm. Dactyl slightly smaller than preceding segments, approximately 1.5 mm by 3 mm, and elongate with pointed distal end (NIGP 126338; Figures 4b, 6a).

Pereiopods 1 to 5 large and well developed. Pereiopod 1 considerably larger than others, propodus and dactylus modified to form large claw (heavily decorated with spines and pits, especially medially), may exceed 40 mm in total length. Carpus reaches maximum length of approximately 10 mm, is rectangular (almost square in some specimens) in shape and usually narrows slightly at proximal end. Merus

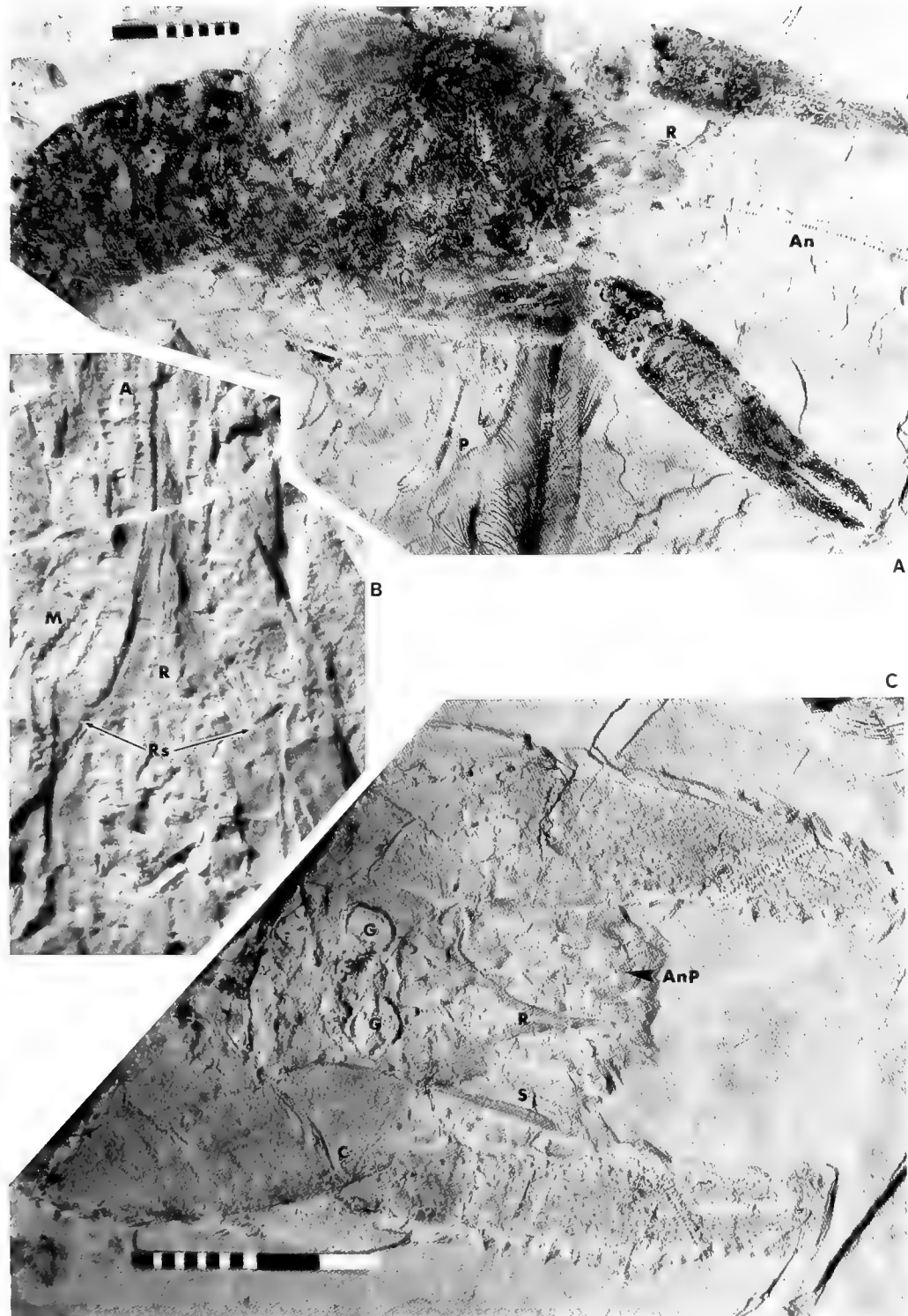


Figure 4. **A.** Lateral view of incomplete specimen (NIGP 126339) of *Palaeocambarus licenti* (with *Lycoperan* fish) (An=antenna, P=pereiopods, R=rostrum). Scale bar=2 cm. **B.** Close up of rostrum, distal end of 3rd maxillipede and antennules of specimen of *P. licenti* (NIGP 126338) (A=antennule, M=third maxillipede, R=rostrum, Rs=rostral spine) $\times 5.4$. **C.** Anterior end of incomplete specimen of *P. licenti* (NIGP 126338) (AnP=antennal peduncle, C=cervical groove, G=gastrolith, R=rostrum, S=scaphocerite). Scale bar=2 cm.

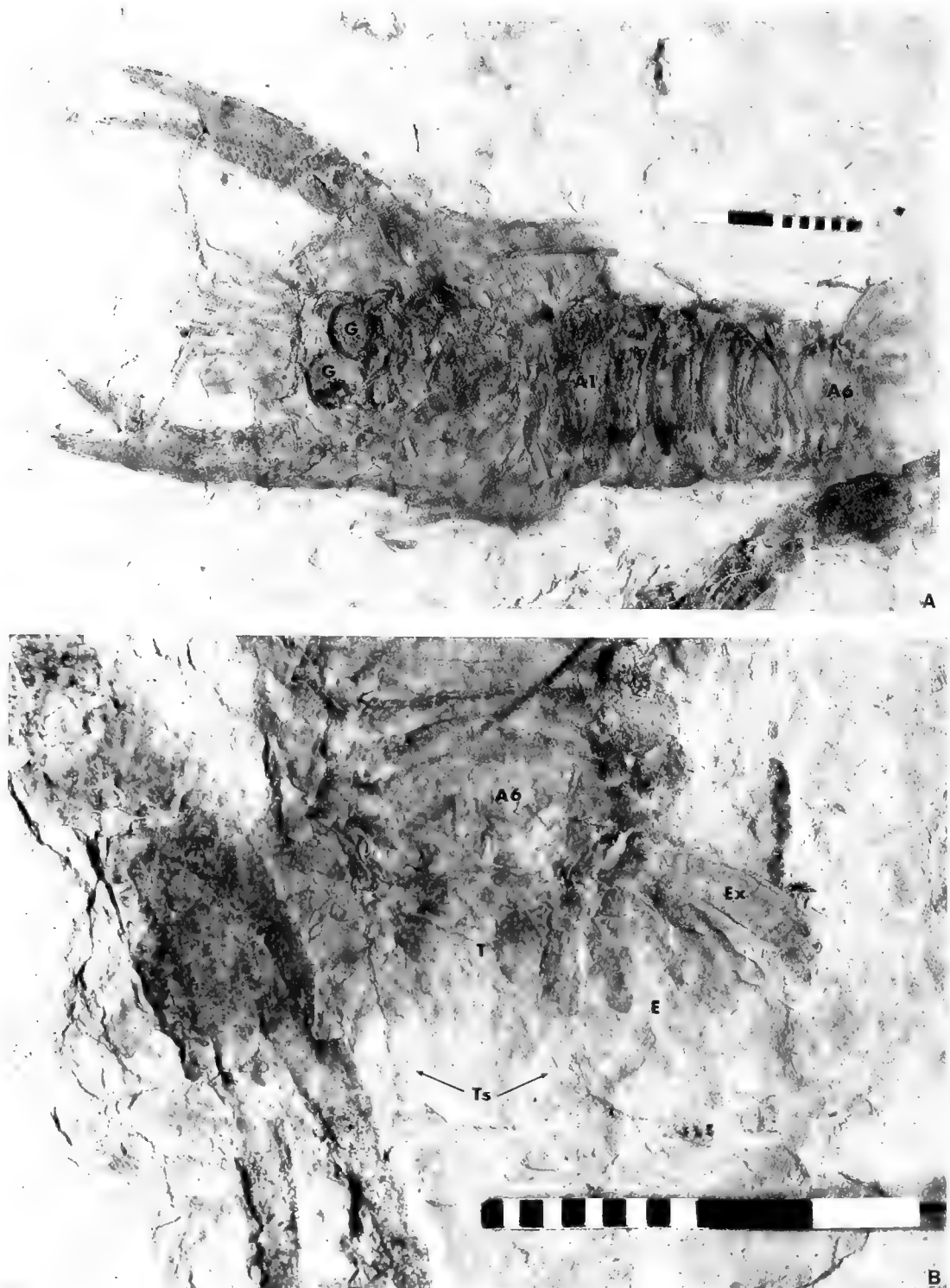


Figure 5. **A.** dorsal view of complete specimen (NIGP 126353) of *Palaeocambarus licenti* (with incomplete chelipede from another specimen) (A1=first abdominal segment, A6 sixth abdominal segment, G=gastrolith). Scale bar=2 cm. **B.** close-up of tailfan of the same specimen (A6=sixth abdominal segment, E=uropodal endopod, Ex=uropodal exopod, T=telson, Ts telson spines). Scale bar=2 cm.

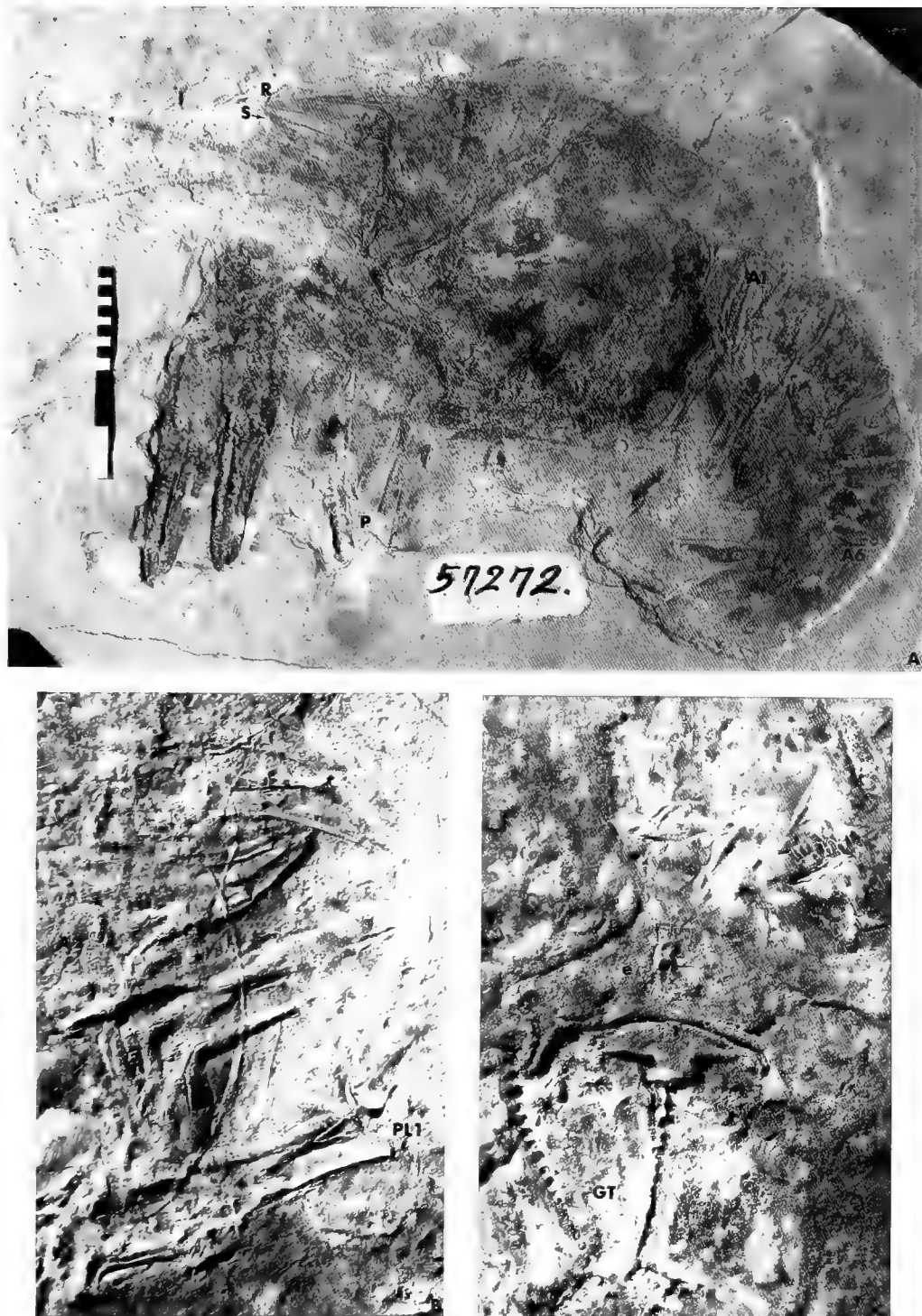


Figure 6. A. Specimen of *P. licenti* from Imaizumi's material (= "*Astacus spinirostris*" : IGP 57272) (A1=first abdominal segment, A6=sixth abdominal segment, P=pereopods, R=rostrum, S=scaphocerite). Scale bar=2 cm. B. Close-up of pleopods of IGP 57272, anterior to bottom (A2=second abdominal segment, PL1=first pleopod). $\times 5.0$. C. Ventral view of anterior end of specimen of *P. licenti* (NIGP 126342) (e=epistome, GT=gastric teeth). $\times 6.4$.

is elongate and approximately one-half the length of propodus (up to 7–8 mm); is rectangular in lateral view but triangular in dorsal view, by far the most common style of preservation seen in this material. Dactylus, propodus, carpus and merus decorated with large spine-like processes, most commonly so on dactyl and propodus. Those on carpus and merus largest, reaching almost 1 mm in width at base (NIGP 126338). Ischium is small and roughly square in shape, showing no sign of hooks. Basis triangular in shape, with rounded proximal margin where it comes into contact with rectangular coxa (NIGP 126339; Figures 4a, 5a, 6a).

Pereiopods 2 to 5 considerably smaller than pereiopod 1, developed as walking legs (as opposed to the chela of pereiopod 1). Coxa possesses lateral distal groove to accommodate basis, is slightly longer than basis (NIGP 126339, 126346). Basis concave distally, forming a groove where it contacts ischium, but is rounded proximally and slightly wider at its distal than proximal end. Ischium short (approximately 0.4 cm) and tapered slightly where it connects with basis. Merus elongate (approx. 1.5–2.0 cm) while carpus considerably shorter (approx. 0.5 cm) and acts as 'knee joint' (NIGP 126339, 126354). In pereiopods 2 and 3, elongate (approx. 1.5 cm) propodus acts with dactylus to form small chelipede at distal end of pereiopod, much smaller than those of 1st pereiopods (NIGP 126339) (Figures 4a, 6a).

Abdomen elongate and rectangular in dorsal view, narrowing slightly distally. Segment length consistent over first 4 segments with largest specimen seen (NIGP 126353) showing lengths of 0.6 mm. Fifth and sixth segments somewhat shorter with lengths of 0.5 and 0.45 mm, respectively (Figure 5a). Pleura rounded and well-developed on tergites 2–5, 2nd expanded slightly posteriorly and thus larger than others. No pleurae seen on tergite 1, pleurae on tergite 6 greatly reduced to accommodate uropods. Sternites reduced in width distally, but sternite/tergite size ratio (sternites being approximately 70 percent as wide as tergites) remains fairly consistent along abdomen. Sternal bars 'bar-belled' in shape, narrow medially but several times wider distally; this results in ovoid gaps, pointed laterally, where arthrodial membranes would have been located in life (NIGP 126353, 126346; Figure 5a).

Circular/ovoid scars evident near antero-lateral regions of sternites. Pleopods elongate, blade-like in shape. There is no evidence of styliform first pleopod in material collected for this study (but see Discussion).

Tailfan very well developed (Figure 5b). Telson large and subrectangular with slightly convex anterior margin. Tapers distally, possesses straight lateral margins, with well-rounded setose distal margin, which is delineated by complete transverse suture. A pair of posteriorly directed spines located just posterior to transverse suture. Uropods are also large, with exopod slightly longer than endopod. Exopod possesses diuresis, is setose along its rounded distal end and along posteriormost portion of lateral margin. Endopod also setose along distal margin (NIGP 126346, 126353).

Etymology.—Van Straelen's specific epithet *licenti* is retained.

Measurements.—Measurements (in mm) are given in Table 1.

Types.—Van Straelen (1928b) indicated his 'nearly complete' specimen in Pl. 1, Figure 1 as the type specimen for *A. licenti*. His material was housed at Hoang Ho Pai Ho Museum, Tientsin, China. Imaizumi's (1938) material (Reg. Nos. 57254, 57267, 57271, 57272 and 57274) is stored in the Institute of Geology and Palaeontology (abbreviated here as IGP), Tohoku University, Sendai, Japan.

Material examined.—New material used in this study includes NIGP (Nanjing Institute of Geology and Palaeontology) 126338–126339, 126341–4 and 126346–126354. Several other uncatalogued specimens are currently in the NIGP collections, some of which were photographed for use in this study (owing to the difficulty in transporting the large slabs upon which these specimens are found or the inferior quality of preservation of several of these specimens). Specimens 57254, 57267 and 57272 from the Institute of Geology and Palaeontology, Tohoku University, Sendai, Japan were also used in this study.

Occurrences.—The material used in the original description of *Astacus licenti* was collected from an unspecified locality, representing Upper Jurassic *Lycoptera/Ephemeroptera* shales, south-west of Shenyang City, Liaoning Province, China. *Astacus spinirostris* was described from material collected from equivalent *Lycoptera* beds in Lingyuan County, Liaoning. The newest material was collected from beds believed to be of equivalent age in Daxinfanzi and Dawangzhangzi villages, Lingyuan County. This locality cannot be described with any greater detail, as these (as well as other) specimens were bought by the Nanjing Institute of Geology and Palaeontology from local farmers, who refused to divulge the exact locations.

Remarks.—The gastric teeth found in this taxon are atypical when compared to those of other crayfish and other decapods in general. Icely and Nott (1992) and Felgenhauer and Abele (1989) have described in considerable detail the foregut morphology as found in various decapod taxa. The physical make-up of the decapod foregut and the gastric mill in particular are particularly complex systems, made up of up to 60 ossicles of varying size and shape. While we are unable to determine the nature of these ossicles in our fossils, we are able to see evidence of the gastric mill elements. It would probably be best described as 'relatively primitive', based on the classification scheme provided by Felgenhauer and Abele (1989). In their 3-tiered system, the most primitive 'type I' foregut possesses heavily sclerotized lateral teeth that work in association with the median tooth to filter and/or masticate food. In their 'type II' foregut, the gastric mill is "completely absent": the median tooth is never present, while the lateral teeth may be replaced by setose lateral ridges. The gastric mill found in *P. licenti* appears to be an intermediate between these two forms: it possesses no medial tooth, but the paired lateral teeth are present and well developed.

However, the system suggested by Felgenhauer and Abele (1989) is derived from studies of the 'lower Decapoda' (including the suborders Dendrobranchiata and Pleocyemata). Recent crayfish are known to possess both a single medial and paired lateral gastric teeth (e.g., Holdich and Reeve, 1988). Thus, what we see with our material is a situation

Table 1. Morphological measurements (in mm) for *P. licenti* and *C. aethus*.

| specimen ^a | cephalothorax length | rostrum length | rostrum width | abdomen length | abdomen width | left exopod length | left exopod width | right exopod length | right exopod width | left endopod length | left endopod width | right endopod length | right endopod width | telson length | telson width | left chelipede length | left chelipede width | right chelipede length | right chelipede width | left chelipede propodus length | right chelipede propodus length |
|-----------------------|----------------------|----------------|---------------|----------------|---------------|--------------------|-------------------|---------------------|--------------------|---------------------|--------------------|----------------------|---------------------|---------------|--------------|-----------------------|----------------------|------------------------|-----------------------|--------------------------------|---------------------------------|
| <i>P. licenti</i> | | | | | | | | | | | | | | | | | | | | | |
| 126338 | | 13 | 17 | | | | | | | | | | | | | 31.5 | 8.5 | 30 | 8 | 15 | 15 |
| 126339 | 38 | 13 | | | | | | | | | | | | | | 35 | 9 | 35 | 9 | 18 | 18 |
| 126341 | | | | | | | | | | | | | | | | 12 | 3 | 12 | 3 | | |
| 126342 | 33 | 10 | 3.5 | | | | | | | | | | | | | 25 | 7.5 | 24 | 7 | 12 | 12 |
| 126343 | | 15 | 7 | | | | | | | | | | | | | | | 45 | 11 | | 23 |
| 126344 | 17 | 6.5 | | | | | | 6 | 2.5 | 4.5 | 2.5 | 4.5 | 2.5 | 4.5 | | | 3.5 | | 3.5 | | |
| 126346 | 26 | 10 | 5 | 29.5 | | 10 | 6 | 10 | 6 | 5 | | | | 8 | 9 | 22 | 6.5 | 23 | 6.5 | 13 | 12 |
| 126353 | 31 | 11 | | 35 | 23 | 13 | | 12.5 | 8.5 | | | 10.5 | 7 | 12 | 10.5 | 27 | 6.5 | 28 | 7.5 | 13 | 14 |
| 57254 | 35 | 11 | 5 | 35 | 26 | 13 | 5 | 14 | 6 | 5 | 10 | 11 | 5 | 13 | 12 | 38 | 11 | 38 | 10 | 13 | 14 |
| 57267 | | | | 24 | | | | | | | | | | | | | | | | | |
| 57272 | 33 | 12 | 4.9 | | | | | | | | | | | | | 23 | 6 | 24 | 6 | 14 | 13 |
| RT129 | 33 | 10 | | 35.5 | 23 | | | 13 | 9 | 11 | 7.5 | 11 | 7.5 | 12 | 10 | 27 | 6.5 | 29 | 7 | 14 | |
| RT130 | | | | | | | | | | | | | | | | 28 | 7.5 | | | 15 | 14.5 |
| RT131 | 44 | 10 | | 33 | | | | | | | | | | | | 35 | 10 | 37 | 10 | 15 | 18 |
| RT132 | | | | 16 | 11 | | | | | | | | | | | | | | | | |
| RT133 | 29 | 11.5 | | 32 | | | | | | | | | | | | 33 | 9 | | | 17 | |
| RT134 | | | | | | | | | | | | | | | | | | | | | |
| RT138 | 28 | 10 | | | | | | | | | | | | | | | | 32 | 8.5 | 12 | 12 |
| RT141 | | | | | | | | | | | | | | | | 23 | 5.5 | 23 | 5 | 13 | 12 |
| RT143 | 30 | 10 | 6 | 31 | | | | 12.5 | 9.5 | 12.5 | 9 | | | | | 17 | 5 | | | 7.5 | |
| RT146 | 21 | | | 24.5 | 16 | | | | | | | | | | | | | 23 | 6.5 | | 12 |
| RT150 | 17.5 | 4.5 | | 23.5 | | | | | | | | | | | | 7.5 | 16 | 17 | 5 | 7.5 | 8.5 |
| <i>C. aethus</i> | | | | | | | | | | | | | | | | | | | | | |
| 126337 | 34 | 9 | 3 | | | | | | | | | | | 8 | 10 | 25 | 8 | 27.5 | 8 | 13 | 13 |
| 126340 | 22 | 7 | | 30 | | | | 7.5 | | | | | | 5 | | 13.5 | | 14.5 | 4 | 8 | 7 |
| 126345 | | | | 24 | | | | 12 | 8.5 | 10 | 6.5 | 11.5 | 10 | | | | | | | | |

possibly reflecting an intermediate state between the three-toothed array seen in recent crayfish and the reduced system seen in many of the 'lower' Decapoda.

Family Cricoidoscelosidae fam. nov.

Type Genus.—*Cricoidoscelosus* gen. nov.

Diagnosis.—Rostrum with rounded base and lateral spines. Bladelike scaphocerite. Well-developed first chelae. No ischial hooks on pereopods. Rounded pleurae. First pleopod styliform in males, remainder annulate. Large telson with large lateral spines.

Etymology.—The name of this family is derived from the Greek words 'cricoides' (meaning 'annular') and 'scelos' (meaning 'leg').

Cricoidoscelosus gen. nov.

Type species.—*Cricoidoscelosus aethus* sp. nov.

Diagnosis.—Rostrum with rounded base and curved lateral spines. Scaphocerite long, bladelike. Chela of first pereopod well developed, highly nodose. No ischial hooks evident. Rounded pleura on abdominal segments 2–5, the 2nd being the largest. Pleopods annulate, with the first specialized as styliform copulatory appendages in males. Female with paired circular 'pores' on 3rd abdominal sternite. Telson with large lateral spines and rounded distal margin.

Etymology.—Same as for the family.

Cricoidoscelosus aethus sp. nov.

Figures 3, 7–8

Diagnosis.—Same as for genus.

Description.—Rostrum elongate, approximately 9 mm in length, narrow and triangular along its anterior two-thirds; posterior third roughly circular in shape. Pair of short, curved spines projects anterolaterally from anterior end of basal portion of rostrum (NIGP 126337 : Figure 7a, b).

Carapace heavily sclerotized, covers thorax completely and partially covers first abdominal segment dorsally, almost completely covers first abdominal segment ventrolaterally due to enlargement (NIGP 126340). Sinusoidal cervical groove present, no other carapace grooves visible. Slight ridge visible along carapace dorsal and lateral margin. Optic notch well developed. Surface of carapace granulate with small spines near anteriormost end of carapace.

Antennules are biflagellate, medial flagellum slightly longer than outer flagellum. Peduncles not completely preserved on any specimens: two distalmost peduncular segments rectangular, approximately 1.5 mm by 1.5 mm. Other peduncular segments are unclear (NIGP 126337, 126340).

Antennae each with single elongate flagellum, longest seen 5.1 cm in length (NIGP 126337). No specimens with complete antennal peduncles, but some segments are preserved. Distalmost segment rectangular in shape, approximately 4 mm², with proximal margin concave. Adjacent segment similar in shape and size but with lateral side extended to approximately 5 mm long. Proximalmost seg-

ment rectangular and elongate, approximately 4 mm wide and 2 mm long. Coxa and basis unclear. Antennal gland present. Scaphocerites elongate, up to 10 mm in length: outer margin straight, inner margin slightly curved. Setal bases present along outer margin (NIGP 126337). Eyes present but not preserved intact: remains found lateral to base of scaphocerites. No peduncle preserved (NIGP 126337).

Epistome v-shaped and directed anteriorly, with anterior process as described for *P. licenti*. However, medial process possesses no pits and is anteriorly directed (NIGP 126337). Gastric structures not evident.

3rd maxillipede well developed, reaching anteriorly to antennal peduncles. Ischium large, 8 mm in length and 3 mm in width, with cristata dentata along inner margin. Merus ovoid, 2 mm wide and 4 mm long. Remaining elements unclear (NIGP 126337).

Pereopod 1 with propodus and dactylus modified to form large claw (up to 25 mm long), decorated with spines and pits distally and medially. Carpus rectangular in shape, up to 7 mm wide and 5 mm long. Merus large and elongate, exceeding 10 mm. Ischium square, lacking hooks. Basis triangular, gently rounded at contact with rectangular coxa (NIGP 126337, 126355).

Pereopods 2 to 5 reduced, developed as walking legs with small distal chelae on 2–3 formed from dactyl and propodus. Coxa slightly longer than basis, 2–3 mm in length. Basis with concave interface with ischium, which is approximately 5 mm long and slightly broader distally. Merus rectangular, may exceed 10 mm in length; carpus also elongate and rectangular, up to 10 mm in length (NIGP 126337, 126355).

Abdomen elongate and rectangular, slightly wider at its anterior. Segment length regular for first 4 segments, with last two slightly shorter in length. Abdominal pleura well developed, posterolaterally oriented. Pleurae absent on tergite 1, reduced on tergite 6 to accommodate uropods. Sternites developed across tergite ventral surface, pointed laterally (NIGP 126337, 126345, 126355).

Pleopod 1 visible in one laterally oriented specimen (NIGP 126355), developed as elongate, styliform appendage, probably utilized as a copulatory structure (as in Astacidae and Cambaridae). Distalmost portion only preserved: approximately 10 mm in length and 3 mm wide at base, tapering to slightly less than 2 mm wide distally. It is simple and undecorated (Figures 8a–b).

Telson large and subrectangular with convex anterior margin; tapers distally, has rounded setose distal margin with complete transverse suture. Pair of posteriorly directed spines adjacent to transverse suture, one on either side of telson. Uropods large, exopod slightly longer than endopod. Exopod and endopod with setose distal margins; exopod also with setose posterolateral margin and diarsis (NIGP 126337, 126345).

Etymology.—The species name is derived from the Greek word 'aethus' (meaning 'unusual').

Type.—Holotype NIGP 126337, paratype NIGP 126355; housed at the Nanjing Institute of Geology and Palaeontology, Academia Sinica, Nanjing, the People's

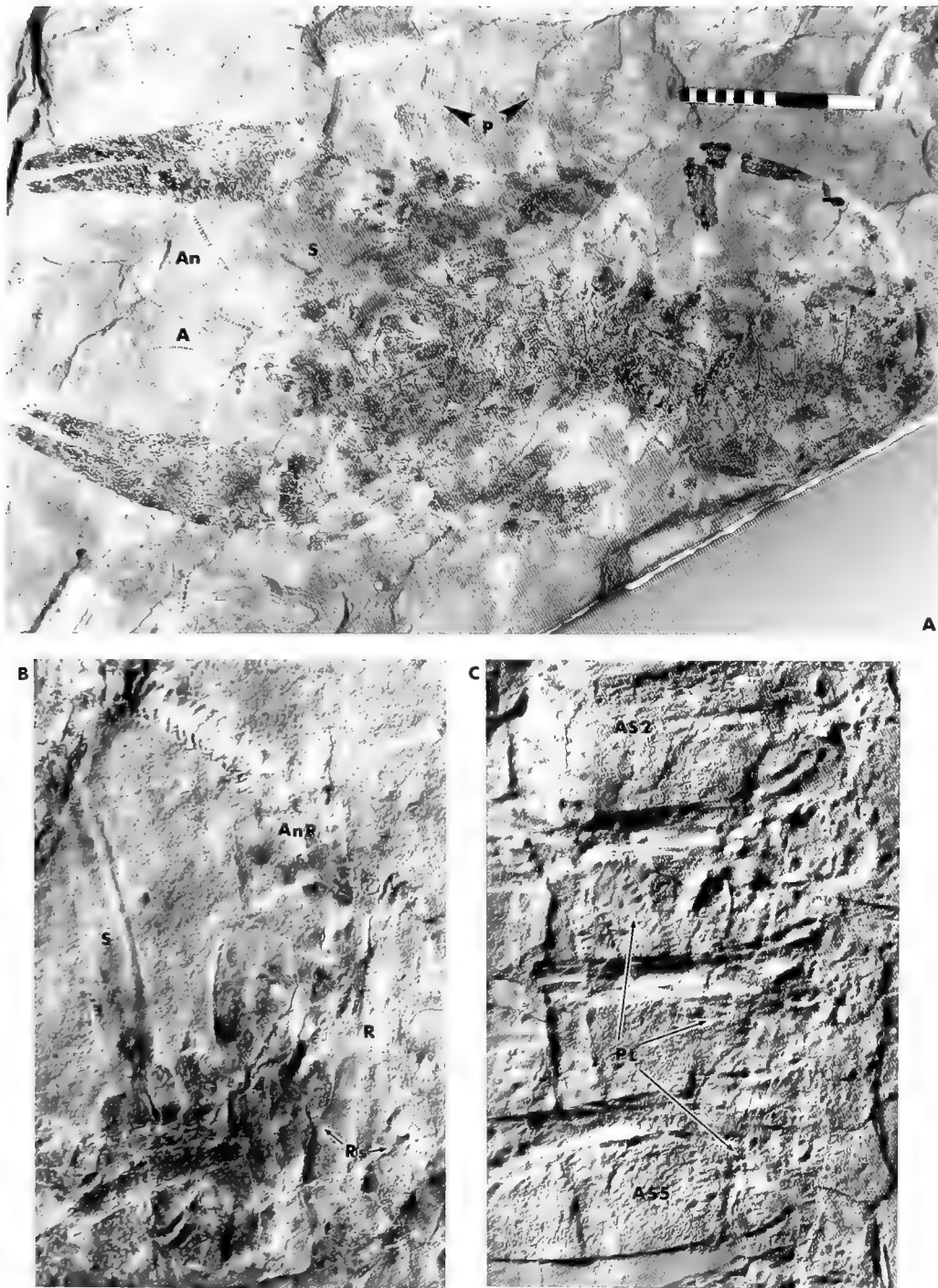


Figure 7. **A.** Ventral view of *Cricoidoscelosus aethus* holotype (NIGP 126337) (A=antennules, An=antenna, P=pereopods, S=scaphocerite). Scale bar=2 cm. **B.** Close-up of ventral view of *C. aethus* (NIGP 126337) (AnP=antennal peduncle, R=rostrum, Rs=rostral spines, S=scaphocerite). $\times 4.9$. **C.** Close-up of ventral view of abdomen with pleopods of specimen of *C. aethus* (NIGP 126345) (AS2=abdominal sternite 2, AS5=abdominal sternite 5, PL = pleopods). $\times 5.4$.

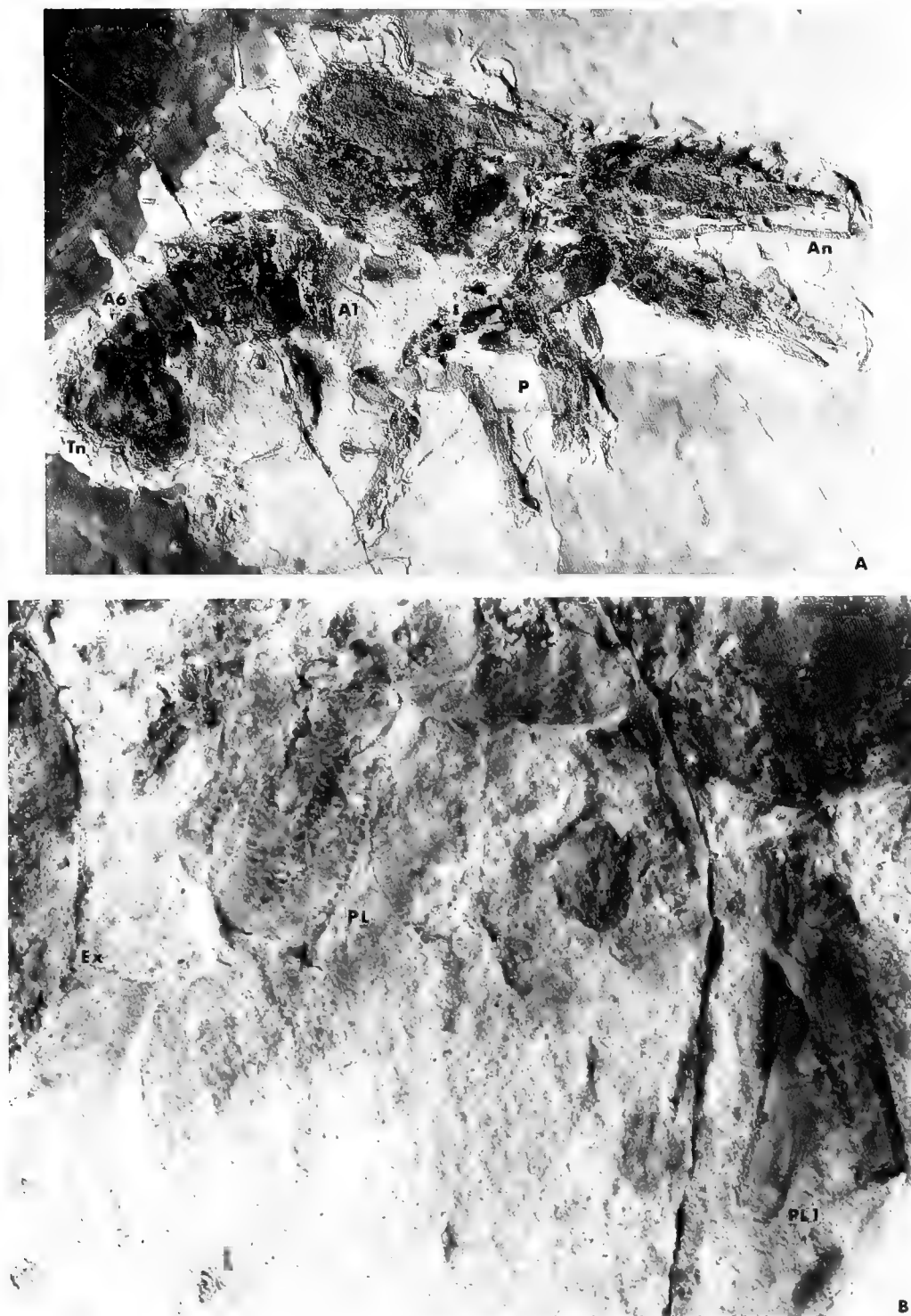


Figure 8. A. Lateral view of *Cricoidoscelosus aethus* paratype (NIGP 126355) (A1=first abdominal segment, A6=sixth abdominal segment, An=antenna, P=pereopods, Tn=tailfan. $\times 0.64$. B. Close-up of pleopods of the same specimen (PL=pleopods, PL1=first pleopod, Ex=uropodal exopod). $\times 4.1$.

Republic of China.

Material examined.—NIGP 126337, 126340, 126345, 126355.

Remarks.—Few specimens exist that can definitively be placed in this taxon from the several specimens in our collections. There is no doubt as to its distinct nature, however, due to its highly characteristic and unique pleopods that are fortunately preserved in several orientations.

Discussion.—A reconstruction of *P. licenti* is provided in Figure 2 while *C. aethus* is shown reconstructed in Figure 3.

Astacus licenti was first described by van Straelen (1928b), based on 3 specimens collected from an unspecified "point south-west of Moukden, in Eastern Mongolia" (actually in north-east Liaoning Province, People's Republic of China). In this description, his assignment of this new species to the genus *Astacus* was "provisional... in the most extensive sense of the genus" (he felt, however, that it belonged "undoubtedly to the family of the Astacidae") (van Straelen, 1928b).

Imaizumi (1938) described a second species, *Astacus spinirostris*, based on two new specimens collected from equivalent *Lycoptera davidii* beds from Niehutzekow, near Lingyuan, China (three specimens of *A. licenti* were also collected at the same time from the region). In his paper, he discussed how both *A. licenti* and *A. spinirostris* are in fact more similar ("particularly in the long slender chelipede and the rounded-off pleural plate") to the fossil form *Pseudoastacus* than to the recent *Cambaroides* [then *Astacus* (*Cambaroides*)] species in Asia (Imaizumi, 1938). Apparently there was, in the minds of both van Straelen and Imaizumi, considerable question as to the definitive generic assignments of these new fossil taxa.

Hobbs (1988) discussed how the chelipedes of *A. licenti* are in fact more similar to the eastern American cambarid genus *Procambarus* than to either *Astacus* or *Cambaroides*; he also suggested that the chelae and the abdominal pleurae of *A. licenti* more closely resemble those of the primitive cambarine genus *Procambarus* than either of the Eurasian genera. These issues, coupled with the discrepancies between the early descriptions and the nature of the fossils examined for this study, were keys that forced us to rethink the taxonomic affinities of this species.

Unfortunately, the key characters used to separate the Astacidae from the Cambaridae (Hobbs, 1974, 1989) are impossible to observe from our material. For example, cyclic dimorphism (present in the Cambaridae, absent in the Astacidae) is impossible to identify in these fossils; and the detailed nature of the 1st pleopod (subtubular distally and lacking ornamentation in the Astacidae, with shallow groove or deep sperm groove and with terminal ornamentation in the Cambaridae) is also not evident in the specimens described here. Our decision to move this taxon from the Family Astacidae to the Family Cambaridae is, then, based on less specific features, such as the absence of astacid crayfish from (and presence of cambarid genera in) the Asian region. The shape of the chelae is another feature mentioned by previous authors (Imaizumi, 1938; Faxon, 1885) as suggesting alternative relationships for *P. licenti*: it has been

compared to the chelae of the extinct *Pseudastacus* and to the recent genus *Procambarus*, presumed to be the most 'primitive' of the cambarid genera (Hobbs, 1988). While we can give no definitive answer to the question of what *P. licenti* may be most closely related to, we feel that these points warrant the movement of this species from the Family Astacidae to the Family Cambaridae.

After examining the original plates of van Straelen (1928b) and Imaizumi (1938) and some of Imaizumi's original material (IGP specimens 57272, 57254 and 57267, Tohoku University, Japan), we determined that several of the features proposed by Imaizumi as distinguishing characters between *A. licenti* and *A. spinirostris* are in fact artifacts of preservation. For example, his 'spines on the mid-dorsal line' of the rostrum appear to be the pair of lateral spines found near the base of the rostrum but viewed from a slightly skewed angle, giving them the appearance of projecting from the middle of the rostrum. These spines are clearly located on the posterolateral region of the rostrum when dorsally preserved specimens are examined, something Imaizumi lacked. The same is true for such features as the shape of the pleural plates and the relative lengths of the exo- and endopods of the uropods: these features appear to lose their usefulness in defining separate taxa when several specimens preserved in multiple orientations are examined.

Imaizumi (1938) also suggested the presence of gastric spines as being a characteristic of *A. licenti* not shared with *A. spinirostris*. This question of the presence/absence of a pair of gastric spines is one that must be addressed here, for several reasons. First, no gastric spines were noted with re-examination of the material described by Imaizumi, removing this character as a potential feature in distinguishing between the previously established taxa from this region. Secondly, a single specimen of the new material examined does possess a set of well-developed, anteriorly directed gastric spines (closely associated with several smaller spines and processes). This specimen is, however, far from complete with only the 'head', anteriormost carapace and first pereopods preserved; thus, it is impossible to compare it with the other specimens with respect to either abdominal or appendage characters. Gastric spines aside, this specimen is largely identical to the other specimens of *P. licenti* examined, suggesting that these gastric spines may not be a species-specific character. They may instead represent a sex-specific character, but this cannot be determined without a better understanding of other sex-specific differences within this species. Another possibility is that they may simply reflect a character that shows flexibility in expression and/or preservation and may vary from individual to individual within a species, as seen in the Palaeozoic pygocephalomorphs (Schram, 1979). Such features would seem to provide no taxonomic information for this material.

The question of sexual dimorphism is further complicated by the narrow range of morphological characters that exhibit a truly dimorphic state in the crayfish. Some dimorphic characters, such as the generally wider abdomen seen in females, are too general to be of any use in a study utilizing fossil specimens. Sexual dimorphism in the Cambaridae, for example, is characterized by several features: males exhibit

cyclic dimorphism with the presence of a sperm groove (and sometimes ornaments such as spines) on the distal portion of the first pleopod, while females possess a seminal receptacle between the 4th and 5th pereopods. In addition, males possess hooks on at least one set of ischia. Sexual dimorphism in the Astacidae is characterized by a lack of cyclic dimorphism and an unornamented subtubular first pleopod in the males, while the females lack a seminal receptacle (Hobbs, 1988). Such features are difficult if not impossible to determine with fossil material.

Such dimorphic features, in general, present a problem with respect to our material. None of our specimens of *P. licenti* possesses a styliform first pleopod: whether this is due to its complete absence in this species, to our having no males in our material, or to this feature simply not being preserved is impossible to evaluate. None of our specimens appears to possess hooks on the ischia; this may be due to our relative lack of males, as suggested earlier, or to the fact that few of our specimens possess well-preserved pereopods. It is possible that perhaps those that we possess are female and thus would have not possessed these ischial hooks.

However, two (IGP 57272, 57254) of the specimens presented by Imaizumi (1938) do possess a pair of styliform first pleopods, whose distalmost segments are unfortunately the only parts preserved. Those of IGP 57272 are preserved laterally and are elongate, slightly curved anteriorly and tapered distally, being 5 mm in length and 1 mm wide at their widest point (Figures 6a, b). IGP Specimen 57254 shows only one of the pair of first pleopods, preserved in ventral view. It is 7 mm long and 1 mm wide, and is slightly laterally directed proximally. No other pleopods are visible on this specimen. These styliform pleopods suggest that this species belongs to either the Cambaridae or the Astacidae (both characterized by the presence of a styliform first pleopod in the males; it is absent in the Parastacidae). We consider these specimens to be males of the species *P. licenti*, supporting again a cambarid/astacid taxonomic position for this genus. Pleopods 2-6 of IGP 57272 are more 'typical' crayfish pleopods, being elongate and blade-like, than the annulate pleopods possessed by *C. aethus*.

The distinct annulate pleopods (2-6) of *C. aethus* are, we feel, sufficiently different from those seen in any other crayfish to warrant placing them in their own family. The presence of styliform first pleopods, however, is an indication that this taxon is related in some degree to at least one (if not both) of the northern hemisphere astacoidean families, Astacidae and Cambaridae.

One phenomenon that is shared by specimens of both *C. aethus* (NIGP 126340) and *P. licenti* (NIGP 126338, 126346, 126353, 126354) is the presence of gastroliths. Those in *P. licenti* are preserved here as moulds of their actual state in recent animals (e.g., Lowrey, 1988), in which the ridged face is the attachment surface to the wall of the cardiac region of the foregut. This is presumed to be the natural state in our animals as well. These gastroliths are present in freshly molted animals and act as calcium storage packages to be reused in the recalcification of the exoskeleton after ecdysis. It is evident that our sample possesses both recently molted

and fully calcified animals. This also is reflected in the general preservation of these animals, as most of the specimens with gastroliths appear to have been less heavily sclerotized than those without gastroliths.

Ortmann [1902; 1905 (summarized in Hobbs, 1988)] made the first attempt to interpret the history of origin, diversification and dispersal for the crayfish, in a synthesis that has remained largely unchallenged until just recently. He suggested that the ancestors of the Potamobiidae (= Astacoidea) and Parastacidae lived in Sino-Australia (and possibly Antarctica) in the Lower Cretaceous, with *Astacoides* reaching Madagascar during the Middle Cretaceous via a Lemurian land-bridge. The Upper Cretaceous saw the splitting of eastern Asia and Australia, resulting in the differentiation of the Potamobiidae in eastern Asia (and then into western North America and Mexico) and the Parastacidae in Australia and Antarctica. In the Lower Tertiary, the genus *Cambarus* arose from *Potamobius* in Mexico, which then spread through eastern North America; while the Parastacidae extended its range through much of South America and Australia, splitting into several genera in the process. During and since the Upper Tertiary, the Potamobiidae moved into western Asia and Europe, with the Parastacidae remaining in South America, Australia and New Zealand. Following Ortmann's reasoning, the ancestor to the crayfish that we recognize today is believed to have originated in a benthic environment similar to that occupied by the modern marine lobsters. From this ancestral stock, three major lines emerged: the extinct Erymidae; the relatively conservative Nephropidae (ancestors of the modern true lobsters); and the highly varied and widely dispersed Astacoidea and Parastacoidea, the true crayfishes.

More recently, however, Scholtz (1995) and Scholtz and Richter (1995) have proposed a closer relationship between the Astacida and the Thalassinida and Meiora than between the Astacida and Homarida. This suggestion is based on phylogenetic systematic studies and a far better understanding of the fossil record for this group. Their research suggests that many of the morphological similarities once cited as uniting the Astacida and the Homarida are in fact plesiomorphic characters, with no true synapomorphies joining these two taxa. Instead, their phylogenetic analysis revealed two characters that support their taxon Fractosternalia (including the Astacida, Thalassinida, Anomala and Brachyura): a movable last thoracic sternite and a pattern of calcified pleural parts connecting thorax and pleon. Scholtz (1995) further goes on to suggest that the invasion into freshwater by the astacoidean ancestor occurred during the Triassic on the "supercontinent" Pangaea. This ancestor then developed into the Parastacidae in the Southern Hemisphere and the Astacidae and Cambaridae in the Northern Hemisphere with the break-up of the Pangaea landmass into Amero-Eurasia and Gondwana.

Our fossil material, dating back to the Jurassic, confirms that crayfish did indeed move into freshwater considerably earlier than the time suggested by Ortmann. However, the features suggested by Scholtz and Richter (1995) as allying the Astacida with the Thalassinida instead of the Homarida are impossible to distinguish with the fossil material at hand.

It may perhaps be interesting to briefly comment on the rationales behind these two suggested evolutionary histories for the 'crayfish'. Ortmann's (1902, 1905) scheme was very much a product of his time, when distributions were believed by many [e.g., Darwin (1859, Chs. 12 and 13) and Wallace (1876; in Hallam, 1994)] to be strictly dispersalist in nature. By his reckoning, crayfish distributions enlarged slowly with the movement of these animals from one point to another and their subsequent establishment in these new territories. He explained problematic distributions, such as the appearance of crayfish on Madagascar, by the presumed presence of land bridges (in this case, a Lemurian land bridge). Scholtz's considerations, on the other hand, are a product of our modern understanding of how plate tectonics or continental drift (Wegener, 1924; in Hallam, 1994) and its association with vicariance biogeography (Croizat *et al.*, 1974) allow for the presence of closely related organisms in isolated localities via the movement of land masses towards and away from each other with time (Hallam, 1994).

Acknowledgments

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Palaeontological Society of Japan (JSP) Standing Committee Actions

During its meeting on January 23, the JSP Standing Committee enacted the following changes to its membership.

New members elected ;

| | | |
|----------------------|----------------------|---------------------|
| Kiyoharu Abe, | Yoshimitsu Ishitobi, | Hirotsugu Kitahara, |
| Takahiro Sato, | Tetsuo Hamada, | Hikoichi Honda, |
| Yukio Miyake, | Kouiti Yazima, | Mitsuko Koike, |
| Tatsuhiko Yamaguchi, | Hidesaku Ishiko, | Akinori Takahashi. |

Resigned members ;

| | | |
|------------------|---------------|-------------------|
| Kaoru Takenami, | Yuji Yamaoka, | Yuriko Matsumura, |
| Tomoyuki Kaneko. | | |

During its meeting on February 27, the JSP Standing Committee enacted the following changes to its membership.

New members elected ;

| | | |
|---------------|--------------------|------------------|
| Kazuo Harada, | Robert G. Jenkins, | Miyuki Misezaki. |
|---------------|--------------------|------------------|

Resigned members ;

| | | |
|-------------------|---------------------|-----------------|
| Haruo Nakasuji, | Shigeru Saito, | Takashi Toyoda, |
| Hidetoki Noguchi, | Yoshiyuki Hirohata, | Sumie Takeda, |
| Tomoyoshi Ito, | Seiichi Komura. | |

During its meeting on May 22, the JSP Standing Committee enacted the following changes to its membership.

New members elected ;

| | | |
|-------------------|--------------------|-----------------------|
| Hideyuki Iwaki, | Naokazu Yoshimoto, | Saburo Sakai, |
| hirotsugu Tajima, | Kazuhiro Sugawara, | Nobutaka Hunayama, |
| Tomoyuki Tajima, | Hideyuki Noguchi, | Yoshitaka Matsuhashi, |
| Yasunori Kano. | | |

Resigned members ;

| | | |
|---------------------|----------------|--------------|
| Satoshi Matsushita, | Kazuyuki Nozu, | Isao Konda, |
| Yen-Nien Cheng, | Setsuji Nagai, | Sueo Naneko. |

行 事 予 定

- ◎第2回日本古生物学会野外ワークショップは、「海産無脊椎動物の古生態学」をテーマとして、1999年9月23日～26日に高知大学を中心として行われます(世話人: 近藤康生・金沢謙一)。参加申込・問い合わせ先: 東京大学総合研究博物館 金沢謙一(電話: 0888-56-0422; Fax: 03-3815-7053; e-mail: kanazawa@um.u-tokyo.ac.jp)
- ◎2000年年会・総会は、2000年1月28日(金)～1月30日(日)に「早稲田大学」で開催されます。一般講演の申し込み締め切りは1999年12月3日です。
- ◎第149回例会(開催予定時期: 2000年の6月末頃)には、「群馬県立自然史博物館」から開催申し込みがありました。
- ◎1999年総会で、2001年からの年会・総会と例会の開催時期の変更が決定されました。年会・総会は6月下旬から7月の初め頃(現在の例会の開催時期)、例会は1月下旬から2月の初め頃(現在の年会・総会の開催時期)開催されます。開催を計画されている機関がありましたら、お申し込み下さい。

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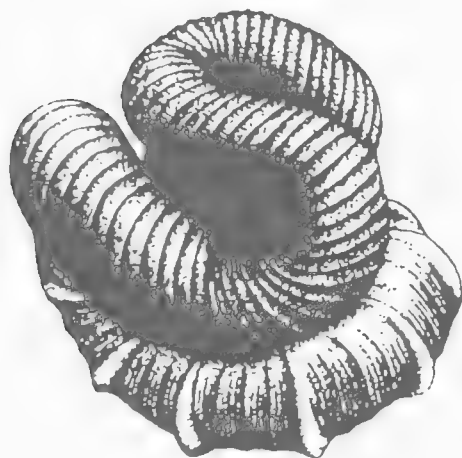
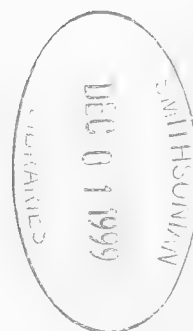
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Cover : Idealized sketch of *Nipponites mirabilis* Yabe, a Late Cretaceous (Turonian) nontoceratid ammonite. Various reconstructions of the mode of life of this species have been proposed, because of its curiously meandering shell form (after T. Okamoto, 1988).

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Papyridea harrimani Dall, 1904 (Bivalvia, Cardiidae) as a marker for upper Eocene and lower Oligocene strata of the North Pacific

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Abstract. Statistical analysis indicates that *Papyridea (Fulvia) nipponica* Yokoyama, 1924, *Papyridea matschigarica* Khomenko, 1938, and *Papyridea matschigarica uspenica* Barinov in Gladenkov *et al.*, 1987, are synonyms of *Papyridea harrimani* Dall, 1904, which was originally described from the lower Oligocene Stepovak Formation in Popof Island, Shumagin Islands, southwestern Alaska. *Papyridea harrimani* occurs only in late Eocene and early Oligocene faunas and is useful for correlating strata from northern Honshu to Alaska: Stepovak Formation, southwestern Alaska; Mallenskaya and Ionayskaya Suites, Koryak Upland; Aluginskaya Suite and lower part of the Pakhachinskaya Suite, eastern Kamchatka; Amaninskaya, Utkholokskaya and Viventekskaya Suites of western Kamchatka; Machigarskaya, Arakayskaya, Gastellovskaya and Akhsnayskaya Suites, Sakhalin; Nuibetsu, Charo and lower Sankebetsu Formations, Hokkaido; Asagai Formation, Honshu. In views of the stratigraphic ranges of *Papyridea harrimani* and other molluscs, strata 3 and 4 of the Pakhachinskaya Suite in eastern Kamchatka may be assigned an age of early Oligocene.

Key words : biostratigraphy, Bivalvia, Cardiidae, Cenozoic, North Pacific, Paleogene, *Papyridea*

Introduction

Marine bivalve molluscs occupy a central position in the Cenozoic stratigraphic framework of the tectonically active North Pacific region from northern Japan to Alaska. Progress in refining this framework has sometimes been inhibited by differing species concepts among Russian, American and Japanese paleontologists. One of the most widespread and biostratigraphically useful bivalve families in this extensive region is the Cardiidae. Kafanov (1997) emphasized the widespread occurrence of a high-latitude North Pacific group of relatively large cardiid species centered around *Papyridea harrimani* Dall, 1904 and *P. matschigarica* Khomenko, 1938. The genus *Profulvia* established by Kafanov (1976) for North Pacific *Papyridea* is considered to be a subgenus of the latter (Kafanov, 1997).

Here we analyze the taxonomic relations between these species and with *Papyridea (Fulvia) nipponica* Yokoyama, 1924, and emphasize the usefulness of this group for broad-scale age control and regional correlations.

Materials and methods

Some of the specimens of *P. matschigarica* examined in this study were collected from the Machigar section in the Schmidt Peninsula, northern Sakhalin, by Y.B. Gladenkov in 1969 and 1979, and by K.B. Barinov in 1996 (Figure 1). The description of the Machigar section we use here is based on a stratigraphic study of the lower part of the Machigarskaya Suite by Y.B. Gladenkov (Barinov and Gladenkov, 1998). We also examined specimens of *Papyridea* in collections of the Central Scientific-Research Geological-Exploration Museum (CNIGRM), St. Petersburg, the All-Russia (formerly All-Union) Petroleum Scientific-Research Geological-Exploration Institute (VNIGRI), St. Petersburg, the Geological (GIN) and Paleontological (PIN) Institutes, Russian Academy of Sciences, Moscow, the University of California Museum of Paleontology, Berkeley, and the California Academy of Sciences, San Francisco, U.S.A.

We have quantitatively defined the main shell characters of *P. matschigarica* by studying numerous topotype specimens, and used statistical analysis to determine the morphological relationships among *P. matschigarica*, *P. mats-*



| Sys tem | Sui- te | Column | Th. (m) | Assemblage | Dominant species | Associated species |
|-----------|----------------|--------|---------|---------------------------------------|--|--|
| MIOCENE | Lower | | 170 | <i>Macoma-Lucinoma</i> | <i>Macoma simizuensis</i> <i>Lucinoma acutilineata</i> | <i>Chlamys donmilleri</i> * <i>Chl. wajampolkensis</i> * <i>Mytilus ochotensis</i> * |
| OLIGOCENE | TUMSKAYA | | 320-340 | <i>Nuculana Delectopecten</i> | <i>Nuculana tumiensis</i> * <i>Delect. watanabei</i> * | <i>Nucula tumiensis</i> * <i>Portlandella nitida</i> <i>Macoma simizuensis</i> <i>Cardiomya majanatschensis</i> * |
| | | | 175 | <i>Periploma</i> <i>Conchocele</i> | <i>Periploma besshoensis</i> <i>Conchocele smekhovi</i> | <i>Acila oyamadensis</i> * <i>Glycymeris nakosoensis</i> |
| | MATCHIGARSKAYA | | 220 | <i>Papyridea Ciliatocardium</i> | <i>Papyridea harrimani</i> * <i>Ciliatocardium matchigarensse</i> | <i>Nemocardium iwakiense</i> *, <i>Trachycardium kinsimarae</i> *, <i>Mya grewinkgi</i> * |
| | | | 35 | <i>Corbicula</i> | <i>Corbicula sitakaraensis</i> *, <i>Mytilus littoralis</i> * | |
| CR. | Up. | | | | | |

Figure 1. Machigar stratigraphic section on the Schmidt Peninsula, northern Sakhalin (type locality of *P. matschigarica*). Legend: *-index species, 1-volcanic rocks, 2-coal, 3-conglomerate, 4-sandstone, 5-siltstone, 6-tuffaceous siltstone, 7-carbonate concretions.

chigarica uspenica, *P. harrimani* and *P. nipponica*. The statistical null hypothesis was reduced to probability analysis of belonging of type-specimens of the above four species to a sampling composed by topotypes of *P. matschigarica*. For that purpose we used the procedure of multidimensional analysis of ejections by sample Mahalanobis distance D^2 (Afifi et al., 1971). The procedure is as follows. Let x_1, \dots, x_k equal a random sampling with distribution $N(\mu, \Sigma)$, and x equal a certain vector of observations with the same distribution. Then

$$D^2 = (x - \bar{X})^T S^{-1} (x - \bar{X})$$

in which \bar{X} and S are the sampling mean and covariance matrix, respectively. The value of $F = [(k-p)/(k^2-1)] \cdot D^2$ has an F -distribution with p and $k-p$ degrees of freedom. The checking procedure for the availability of ejections among the observation data utilizes F -statistics in which \bar{X} and S are calculated from a subset of vectors of the same sample, which has already been checked for ejections. Each of the four variables was preliminarily tested for Gaussian distribution based on χ^2 and Kolmogorov-Smirnov

criteria. All the variables proved to be normally (Gaussian) distributed and required no transformation of the initial data.

The shell characters referred to herein are: L =shell length, H =shell height, B =convexity of one valve (all dimensions in mm), R =number of radial ribs. The dimensions of the holotypes given here differ somewhat from those in the original descriptions, owing to differences in shell orientation during measurement (see Kafanov et al., 1997; Kafanov, 1998).

Results

The nominal species to be described below form a morphologically coherent group consisting of *P. harrimani*, *P. nipponica*, *P. matschigarica* and *P. matschigarica uspenica*. Each is discussed separately.

Papyridea (Profulvia) harrimani Dall, 1904

Figures 2-1, 4-6; 3-1-5

Papyridea harrimani Dall, 1904, p. 114, pl. 10, fig. 5.

Type locality.—Coastal bluffs on the north shore of Popof Island, Shumagin Islands, southwestern Alaska. Stepovak Formation, lower Oligocene.

Depository of the type material.—Holotype, U.S. Natl. Mus. no. 164867.

Comments.—This was originally described as a Miocene species by Dall (1904; see also Schuchert *et al.*, 1905), who thought that the type-locality of *P. harrimani* in Popof Island was correlative with beds in adjacent Unga Island (Figure 4), to which he erroneously assigned a Miocene age. These Unga Island strata were later determined to be largely nonmarine and to contain no molluscs (Marincovich and Wiggins, 1991). Dall's (1904) mollusc collections that are purportedly from these Unga Island strata contain an artificially mixed fauna of Miocene and Oligocene species (MacNeil *et al.*, 1961). Assignment of a Miocene, or possible Miocene age to the Unga Island strata (Dall, 1896, 1904) was repeated by later workers (Schuchert *et al.*, 1905; Burk, 1965; Detterman *et al.*, 1996). The exclusive presence of Oligocene molluscs with *P. harrimani* in the strata of Popof and Unga Islands assigned to the Stepovak Formation has been verified by one of us (Marincovich, 1988, 1989, 1990; Marincovich and McCoy, 1984) during field studies. The early Oligocene age of the Unga Island beds with *P. harrimani* was established by Marincovich and Wiggins (1991) on the basis of dinoflagellates and a potassium-argon age of 31.3 ± 0.3 Ma from biotite in a tuff bed. In the nearby Popof Island, the type-locality of *P. harrimani*, the Stepovak Formation contains the same molluscan fauna as in the Stepovak strata on Unga Island and is undoubtedly of early Oligocene age.

Distribution.—Lower Oligocene, Stepovak Formation at East Head stratigraphic section, Popof Island (type-locality), and West Head stratigraphic section, Unga Island, Shumagin Islands, southwestern Alaska (Dall, 1904; MacNeil in Burk, 1965; Marincovich, 1989). Oligocene Asagai Formation of Honshu. In Japan *P. harrimani* is reported also from the upper Eocene Sakasagawa (=lower Sankebetsu) Formation of the Haboro coal-field, Hokkaido (Noda, 1992a) and from the Paleogene Charo Formation of the Kushiro coal-field, Hokkaido (Honda, 1989). The ages of the Sakasagawa and Charo Formations are controversial. Prof. K. Ogasawara (pers. comm. to A. Kafanov, June 12, 1997) informs us that the Sakasagawa Formation is a tentative name for strata which were previously included in the Sankebetsu Formation. Noda (1992a) reported *P. harrimani* from the Sankebetsu Formation (then of presumed Miocene age), and he divided the Sankebetsu Formation of previous workers into the Sakasagawa Formation and the Sankebetsu Formation. Based on planktonic foraminifers and calcareous nannofossils, the Sakasagawa Formation is now assigned an Eocene age, even though presumed Miocene molluscs (*Anadara* and *Dosinia*) are reported in the upper part of the Sankebetsu Formation (Noda, 1992b). Honda (1989) reported an

Oligocene age for molluscs of the Charo Formation, although planktonic foraminifers (Kaiho, 1984) and calcareous nannofossils (Saito *et al.*, 1984) suggest an Eocene age.

"*Papyridea harrimani*" cited from the middle Miocene Ainonai Formation in Hokkaido (Uozumi *et al.*, 1966, p. 177, pl. 15, figs. 1, 7) cannot be reliably assigned to this species, and more closely resembles *Papyridea (Profulvia) kurodai* Sawada, 1962.

Papyridea (Profulvia) nipponica Yokoyama, 1924*Papyridea (Fulvia) nipponica* Yokoyama, 1924, p. 17, pl. 3, figs. 3, 4.

Type locality.—Tatsuta coal-field, Futaba District, Fukushima Prefecture, Honshu. Asagai Formation, Oligocene.

Depository of the type material.—Lectotype (designated as holotype by Hatai and Nisiyama, 1952, p. 105), CM 22090—University Museum, University of Tokyo, missing. It was refigured by Makiyama (1957, pl. 13, figs. 4, 4a) and by Kafanov (1997, pl. 1, fig. 7).

Distribution.—Known only from Asagai Formation of Fukushima Prefecture, Honshu (Kamada, 1962).

Comments.—This species has been synonymized with *P. harrimani* Dall, 1904 by most Japanese paleontologists (e.g. Oyama *et al.*, 1960), with the exception of Kamada (1962) and Masuda and Noda (1976).

Papyridea (Profulvia) matschigarica Khomenko, 1938

Figures 2-2, 3

Papyridea matschigarica Khomenko, 1938, p. 47, pl. 7, figs. 5-7; pl. 8, fig. 6; pl. 9, fig. 7.

Type locality.—Between Cape Marii and Monchigar Bay, Schmidt Peninsula, Okha Province, Sakhalin. Lower part of Machigarskaya Suite, upper ? Eocene-lower Oligocene.

Depository of the type material.—Lectotype (designated by Slodkewitsch, 1938, p. 407), CNIGRIM no. 81/5044.

Distribution.—Upper Eocene and lower Oligocene of Far-eastern Russia. Upper Eocene Takaradayskaya Suite and lower part of Machigarskaya Suite of Sakhalin. Lower Oligocene Machigarskaya, Arakayskaya, Akhsnayskaya and Gastellovskaya Suites of Sakhalin; Mallenskaya and Ionayskaya Suites of the Koryak Upland; Amaninskaya Suite of western Kamchatka.

Comments.—According to Slodkewitsch (1938, p. 408), Khomenko (1938, p. 48) noted the wide morphologic variability of this species, along with the similarity of some young individuals to *P. nipponica* and *P. harrimani*, and inferred that "... under the name of *P. nipponica* and *P. harrimani* only young specimens of *P. matschigarica* were described". This inference has yet to be substantiated, although the close relationship between these species is quite evident. *P. harrimani* Dall and *P. nipponica* Yokoyama are easily distinguishable from *P. matschigarica* by their much smaller size, more equilateral contour and smaller number of ribs. Following Slodkewitsch (1938), nearly all Russian authors have considered *P. matschigarica* to be a separate species, even though its shell shape (Figure 5) is similar to that of large *P.*



harrimani. In fact, Makiyama (1934) described Machigarian specimens under the name *P. harrimani*.

***Papyridea (Profulvia) matschigarica uspenica* Barinov in Gladenkov et al., 1987**

Figures 3–6—8

Papyridea matschigarica uspenica Barinov in Gladenkov et al., 1987, p. 39, pl. 13, figs. 9, a, b, 22.

Type locality.—Ugol'naya River, coast of the Gulf of Korf, eastern Kamchatka. Aluginskaya Suite, bed 1, Oligocene.

Depository of the type material.—Holotype, PIN no. 1/1–1.

Distribution.—Oligocene to lower(?) Miocene of Kamchatka. Aluginskaya and Pakhachinskaya Suites of eastern Kamchatka.

Facies-related variability of *Papyridea matschigarica*

Table 1 and Figure 5 both support Khomenko's (1938) conclusion concerning the wide variability of *P. matschigarica* and very close morphological relationships among all considered *Papyridea* species.

The distribution of *P. matschigarica* in the Machigar section of the Schmidt Peninsula, northern Sakhalin (Figure 1) is as follows. *P. matschigarica* first appears virtually at the base of the Machigarskaya Suite in fine grey pebble conglomerates (up to 2 m in diameter) directly overlying a sand- and coal-bearing member (30–32 m thick) that contains remnants of *Mytilus littoralis* Slodkewitsch, *Corbicula sitakaraensis* Suzuki and *Cerithidea quadrimonilicosta* Khomenko. At a horizon 45–50 m above the base of the section, *P. matschigarica* occurs in flat-lying strata (up to 85 m thick) of alternating conglomerate (0.5–1 m in diameter), sandstone and claystone (3–5 m thick), and in a superjacent strata (up to 80 m thick) of alternating sandstone (1.5–2 m thick) and claystone (3–14 m thick).

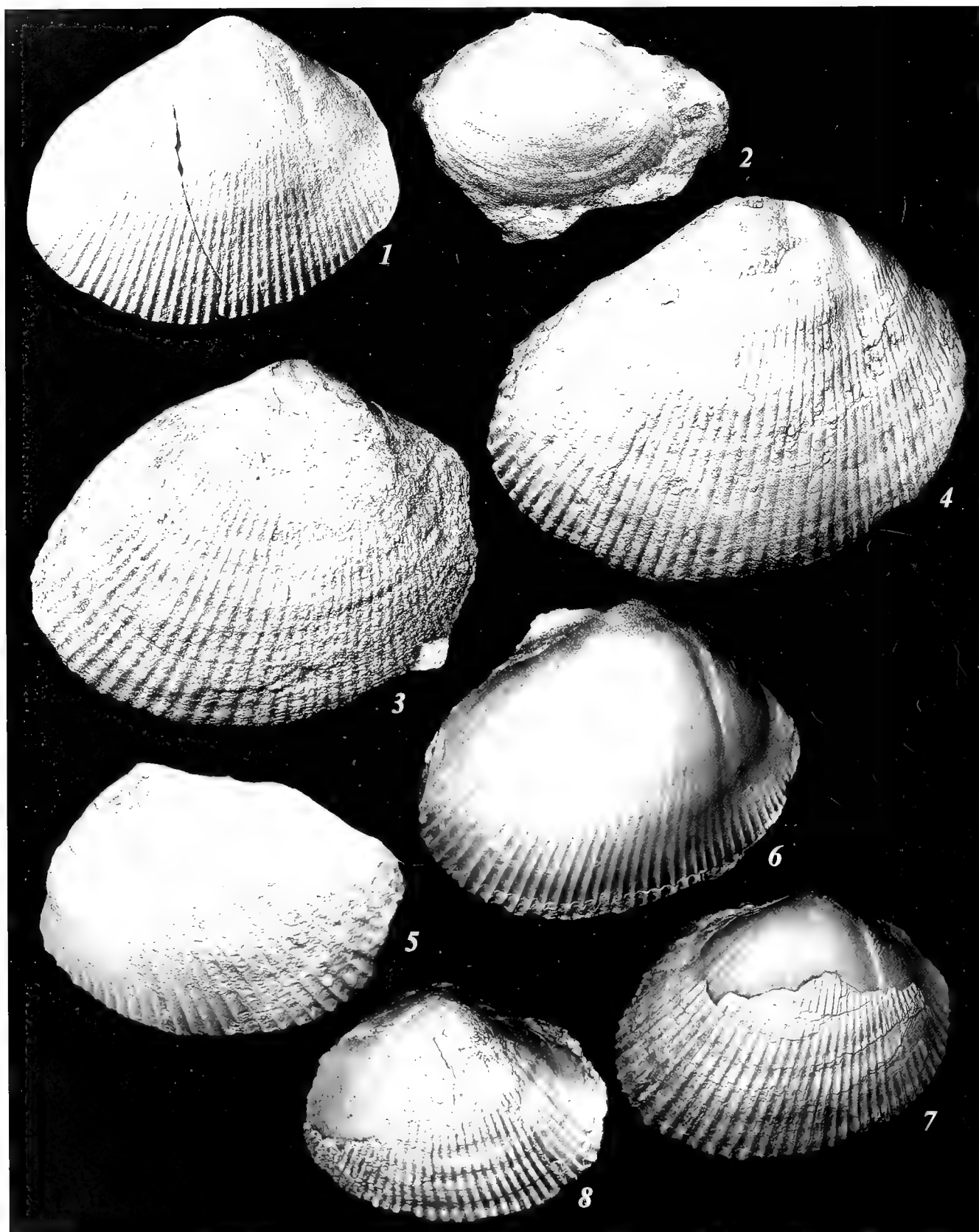
In the part of the Machigar stratigraphic section described above, *P. matschigarica* occurs only in beds of fine pebbly conglomerate and conglomeratic sandstone associated with the following molluscs: *Nemocardium iwakiense* (Makiyama), *Mya* cf. *grewingki* Makiyama, *Thracia schmidtii* Krishtofovich, *Pododesmus schmidtii* Krishtofovich, *Trachycardium kinsimarae* (Makiyama), *Chlamys matchgarensis* Makiyama, *Modiolus matchgarensis* (Makiyama), ? *Megacardita matschigarica* (Khomenko), *Yoldia matschigarica* Krishtofovich, *Y. caudata* Khomenko, *Ciliatocardium asagaiense* (Makiyama), *Laevicardium taracaicum* (Yokoyama), *Liocyma furtiva* (Yokoyama), *Arca sakamizuensis* Hatai and Nisiyama, *Neptunea ezoana* Takeda, and *Turritella importuna* Yokoyama. *In situ* specimens of *P. matschigarica* are mostly molds of single

valves, with some molds of paired valves, and their chaotic orientation indicates post-mortem transport. Specimens in the lowest 75 m of the Machigar section are almost identical in size and shape with the holotype of *P. harrimani* (Figure 5). Higher in the section the same *Papyridea* is abundant in fine pebbly conglomerate and conglomeratic sandstone. However, these specimens are larger in size and more distinctly convex, and they most closely resemble the holotype of *P. matschigarica*. An increase in their average shell size toward the top of the Machigar sequence seems to correlate with a gradual reduction in the proportion of coarse clastics. The type locality of *P. matschigarica* evidently lies in the upper part of the lower member of the Machigarskaya Suite (see Khomenko, 1938). In our opinion, the size and shape differences seen in *Papyridea (Profulvia)* from the upper and lower parts of the Machigar section are related to differences in ecological conditions such as substrate and depth. Conglomerates with a shallow-water molluscan fauna contains "*P. harrimani*," whereas sandstones with deeper-water molluscs contain "*P. matschigarica*" (Figure 5). The number of ribs varies widely and is highly dependent on shell preservation. Most specimens are molds that do not allow for accurate rib counts, because they often lack ribs on their anteriormost and/or posteriormost portions. It should also be noted that in many present-day Cardiidae (subfamily Clinocardiinae), a difference in the number of ribs to the extent of 10–12 is considered to be in the realm of intraspecific variation, including ontogenetic variation (e.g., Kafanov, 1981, 1998). A statistical analysis of basic shell dimensions for the type specimens of *P. matschigarica*, *P. matschigarica uspenica*, *P. nipponica* and *P. harrimani*, and in topotypes of *P. matschigarica* (Figure 5), clearly shows that they all belong to one general group (Table 2). These data suggest that *P. matschigarica*, *P. matschigarica uspenica* and *P. nipponica* are junior synonyms of *P. harrimani*. It is especially notable that the holotype of *P. harrimani* is more closely related in form to topotypes of *P. matschigarica* than the lectotype of *P. matschigarica* (Table 2).

Discussion

P. harrimani s.l. occurs in upper Eocene to lower Oligocene strata over a wide area of the high-latitude North Pacific, from southwestern Alaska to Hokkaido and northern Honshu. Based on these occurrences, correlations may be made between the following strata: Stepovak Formation, southwestern Alaska; Mallenskaya and Ionayskaya Suites, Koryak Upland; Aluginskaya Suite and lower part of the Pakhachinskaya Suite, eastern Kamchatka; Amaninskaya, Utkholokskaya and Viventetskaya Suites of western Kamchatka; Machigarskaya, Arakayskaya, Gastellovskaya and Akh-

Figure 2. 1a, b. Holotype of *Papyridea harrimani* Dall, 1904. North shore of Popof Island, southwestern Alaska; Stepovak Formation. U.S. Natl. Mus. no. 164867. 2. Lectotype of *Papyridea matschigarica* Khomenko, 1938. Between Marii Cape and Monchigar Bay, Schmidt Peninsula, Okha District, northern Sakhalin; lower part of Machigarskaya Suite. CNIGRM no. 81/5040. 3. Paralectotype of *Papyridea matschigarica* Khomenko, 1938. The same locality as on Fig. 2–2. CNIGRM no. 85/5044. 4. *P. harrimani*. Nairo River, eastern Sakhalin, analog of Machigarskaya Suite. CNIGRM no. 103/6818. 5. *P. harrimani*. The same locality as on Fig. 2–4. CNIGRM no. 104/6818. 6. *P. harrimani*. Schmidt Peninsula, northern Sakhalin, Machigarskaya Suite. PIN no. 90/3962. All figures shown natural size.



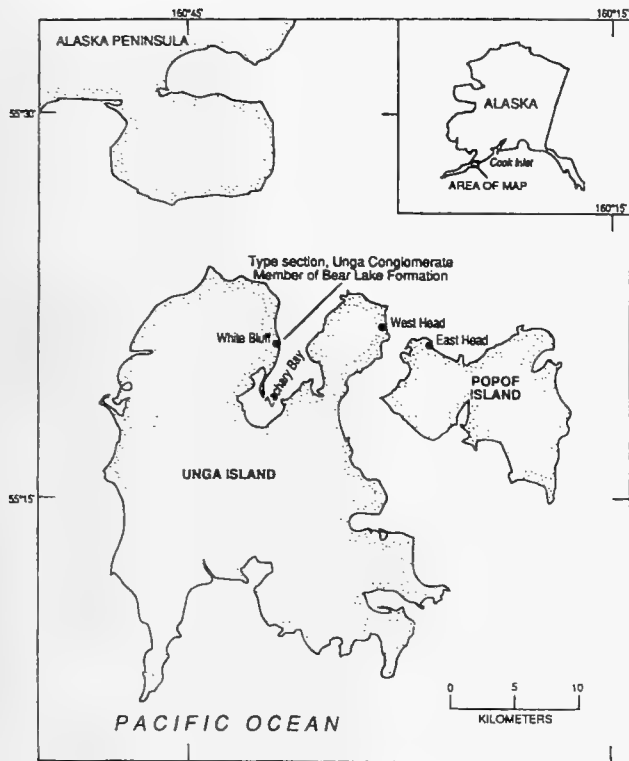


Figure 4. Index map showing the type section of Unga Conglomerate and the type locality (East Head) of *Papyridea harrimani*.

snayskaya Suites, Sakhalin; Nuibetsu, Charo and lower Sankebetsu Formations, Hokkaido; Asagai Formation, Honshu. These many occurrences of *P. harrimani* allow us to judge it as a significant marker for upper Eocene to lower Oligocene strata of the North Pacific.

This conclusion may at first seem to contradict the pres-

ence of *P. matschigarica uspenica* in beds 3 and 4 of the Pakhachinskaya Suite of the main Gulf of Korf section (Ugol'naya River), and in beds 5 and 6 of an additional section (Bol'shaya Medvezhka River), both of which were assigned to the early and middle Miocene by Gladenkov *et al.* (1987). However, we suggest that the stratigraphic distribution of many common bivalve species in Japan and Sakhalin argues for assigning the middle part of the Pakhachinskaya Suite in eastern Kamchatka (beds 3 and 4 along the Ugol'naya River) to the lower Oligocene. The molluscan fauna of the Pakhachinskaya Suite in this part of the Gulf of Korf section is comparable to the faunas of the Asagai Formation in the Joban coal-field, Honshu, the Utkholokian and Viventekian horizons of western Kamchatka (see also Gladenkov, 1992), and the Machigarian and Kholmskian horizons of South Sakhalin (see Kafanov and Savizky, 1995).

Thus, beds 3 and 4 of the Pakhachinskaya Suite of eastern Kamchatka characteristically contain *Ciliatocardium asagaiense* (Makiyama) and *Thracia kidoensis* Kamada, which Japanese workers (Mizuno, 1964; Honda, 1986) have described as representatives of the Asagai-Poronai fauna (Otuka, 1939). The Asagai-Poronai fauna contains planktonic foraminifers as old as Eocene (Ibaraki, 1986). The consideration of a precise Paleogene age for beds 3 and 4 of the Pakhachinskaya Suite also involves "*Cardium esutoruensis*" mentioned by Gladenkov *et al.* (1987) for bed 4 of the Pakhachinskaya Suite; this species should rather be referred to as *Laevicardium tristiculum* (Yokoyama) (Kafanov and Amano, 1996). The *Laevicardium tristiculum* (= *Cardium esutoruensis*) bearing horizon was established in Sakhalin as a marker of the Arakayskaya Suite and its correlatives by Krishtofovich (1954, 1964) and by Margulis and Savizky (1969). The Asagai Formation in the Joban coal-field of central Honshu contains *Laevicardium tristiculum*. According to Yanagisawa *et al.* (1989), the age of the Shiramizu Group, which includes the Asagai Formation, is early Oligocene according to its diatom flora, molluscs and mammals. In the Ugleorsk Province of southwestern Sakhalin, *L. tristiculum*

Table 1. Measurements (in mm) of type specimens of *Papyridea (Profulvia) harrimani*, *P. (P.) nipponica*, *P. (P.) matschigarica* and *P. (P.) matschigarica uspenica*.

| Species (subspecies) | Shell length | Shell height | Convexity of one valve | Number of radial ribs |
|----------------------------------|--------------|--------------|------------------------|-----------------------|
| <i>P. harrimani</i> | 48.0 | 40.0 | 9.5 | 42 |
| <i>P. nipponica</i> | 69.7 | 51.3 | 13.0 | 52 |
| <i>P. matschigarica</i> | 95.0 | 76.4 | 20.3 | 55 |
| <i>P. matschigarica uspenica</i> | 70.0 | 59.0 | 18.0 | 47 |

Figure 3. 1. *Papyridea harrimani* Dall, 1904. Schmidt Peninsula, northern Sakhalin, Machigarskaya Suite. PIN no. 90/3962. 2. *P. harrimani*. Machigar section of the Schmidt Peninsula, site 4/7, GIN no. 3618/1. 3. *P. harrimani*. Machigar section of the Schmidt Peninsula, site 5/29, GIN no. 3618/2. 4. *P. harrimani*. Machigar section of the Schmidt Peninsula, site 5/24, GIN no. 3618/3. 5. *P. harrimani*. Machigar section of the Schmidt Peninsula, site 2/15, GIN no. 3618/4. 6. Paratype of *Papyridea matschigarica uspenica* Barinov in Gladenkov *et al.*, 1987. Ugol'naya River, Gulf of Korf section, eastern Kamchatka, site 10/2-3. Pakhachinskaya Suite. GIN no. 3669/3. 7. Paratype of *Papyridea matschigarica uspenica* Barinov in Gladenkov *et al.*, 1987. Ugol'naya River, Gulf of Korf section, eastern Kamchatka, site 10/2-5. Pakhachinskaya Suite. GIN no. 3669/4. 8. Paratype of *Papyridea matschigarica uspenica* Barinov in Gladenkov *et al.*, 1987. Bol'shaya Medvezhka River, Gulf of Korf section, eastern Kamchatka, site 18/7. Pakhachinskaya Suite. GIN no. 3669/7. All figure shown natural size.

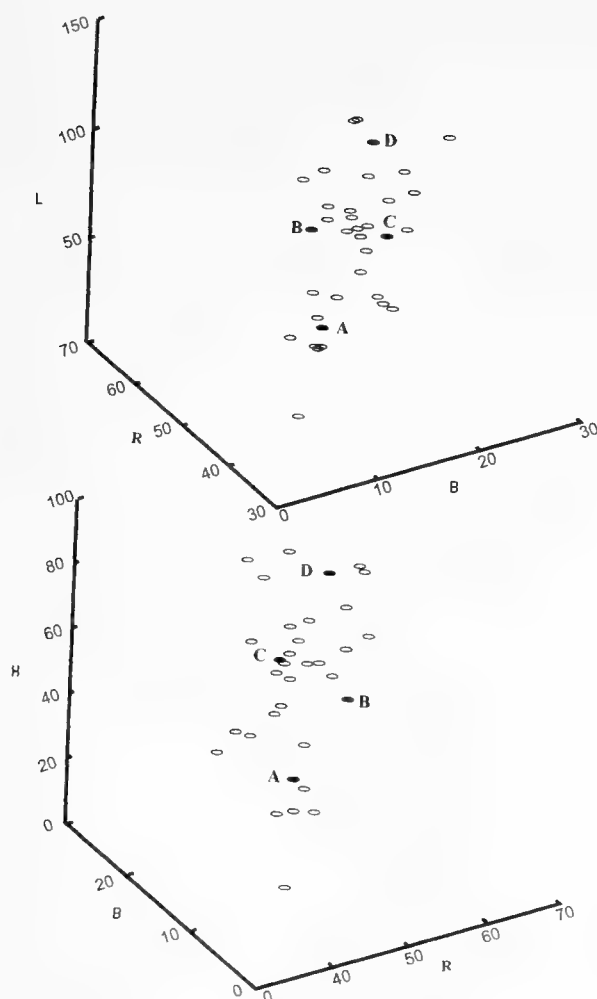


Figure 5. Location of type specimens of *Papyridea harrimani* (A), *P. nipponica* (B), *P. matschigarica uspenica* (C) and *P. matschigarica* (D) in space of characters of *P. matschigarica* topotypes from lower (dotted circles) and upper (white circles) parts of the Machigar section in northern Sakhalin. Abbreviations: L=shell length (in mm); H=shell height (in mm); B=convexity of one valve (in mm); R=number of radial ribs.

Table 2. Probability of assignment of type specimens of *Papyridea matschigarica*, *P. matschigarica uspenica*, *P. nipponica* and *P. harrimani* to sampling of topotypes of *P. matschigarica*. Probabilities $P(D^2)$ of assignment to sampling of each topotype account for the range between 0.998 and 0.131; $P(F)$ between 0.997 and 0.066.

| Type specimens | $P(D^2)$ | $P(F)$ |
|----------------------------------|----------|--------|
| <i>P. harrimani</i> | 0.780 | 0.816 |
| <i>P. matschigarica uspenica</i> | 0.749 | 0.790 |
| <i>P. matschigarica</i> | 0.696 | 0.745 |
| <i>P. nipponica</i> | 0.653 | 0.707 |

has been found in the upper member of the Arakayskaya Suite. Okamura (1994) assigned a K-Ar age of 38.6 Ma and 30.6 Ma to the lower and middle parts of the Arakayskaya Suite respectively. Thus, in terms of molluscs, strata 3 and 4 of the Pakhachinskaya Suite in eastern Kamchatka may be assigned in age to early Oligocene.

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Upper Paleozoic biostromes in island–arc carbonates of the eastern Klamath terrane, California

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Abstract. The eastern Klamath terrane (eKt) of California, a geographically isolated, island-arc area, was invaded by biostromal communities during three intervals of carbonate deposition in the Carboniferous and Permian. Visean/Serpukhovian biostromes were formed on short-lived carbonate banks by the Tethyan brachiopod *Striatifera* and phylloid algae. Bashkirian biostromes on similar banks were formed by the cosmopolitan microproblematica *Tubiphytes* and *Donezella*. Wolfcampian biostromes occur in a thick carbonate platform and slope section and were formed by *Tubiphytes*, the phylloid alga *Eugonophyllum*, and *Palaeocaplysina*, an enigmatic taxon known mainly from Laurentia. Species diversity of biostrome dwellers increased from the Early Carboniferous to Early Permian, when it reached the level of high-diversity shelf-mud communities. Biostromes in the eKt record the global recovery of Carboniferous–Permian reef biotas during temporal intervals of quiescent volcanism that permitted carbonate deposition.

Key words : biostromes, California, Carboniferous, island–arcs, Permian

Introduction

The Late Paleozoic, noted for its paucity of frame-building metazoans, was an interval of ecologic recovery of reef communities following their collapse in the Late Devonian extinctions (Sheehan, 1985 ; Copper, 1988). Island-arc carbonates of the eastern Klamath terrane, California (Figure 1), offer a picture of this recovery in a setting of geographic isolation, limited availability of favorable environments, and recurring biogeographic invasions from outside areas. Although no Late Paleozoic reefs or mound-like structures are known from the terrane, several reef-forming taxa are locally abundant in tabular limestone beds that represent biostromes. Biostrome formation was dominated by binding, baffling, and production of skeletal grains, and biostromal taxa included a mixture of algae, problematica and brachiopods (Figure 2).

Geologic setting

Devonian through Early Jurassic rocks of the eastern Klamath terrane (eKt) formed in a succession of island-arcs and arc-related basins (Albers and Bain, 1985 ; Renne and Scott, 1988 ; Miller, 1989). Renne and Scott (1988) summarized paleomagnetic data for the eKt, which indicate paleolatitudes equivalent to cratonic North America since at least Permian times. Paleozoic longitudinal position of the eKt with respect to North America has been a matter of debate. Miller (1987), Rubin *et al.* (1990), Miller and Saleeby (1991), Miller *et al.* (1992), and Darby *et al.* (1997) placed the

eKt near the western margin of cratonic North America, based on provenance of detrital zircons and stratigraphic ties with adjacent terranes. In contrast, Stevens *et al.* (1990) and Belasky and Runnegar (1994) concluded that the eKt formed in an oceanic setting thousands of km west of North America, based on Permian faunal composition and biogeographic models. In either scenario, the eKt represents an isolated area of shallow marine environments in the Paleozoic. Like a number of Cordilleran terranes (Soja, 1996), it contains a mixture of cosmopolitan, endemic, Tethyan and North American taxa (Watkins and Wilson, 1989 ; Watkins *et al.*, 1989 ; Potter *et al.*, 1990 ; Stevens *et al.*, 1990 ; Noble and Renne, 1990).

Upper Paleozoic stratigraphy and carbonates

Early to Middle Devonian arc construction in the eKt was followed by extension and development of a large, arc-related basin in which submarine fan sequences of the Upper Devonian to Lower Carboniferous Bragdon Formation were deposited (Watkins, 1986, 1990 ; Miller and Cui, 1987 ; Miller and Saleeby, 1991). Volcaniclastic deltaic sediments with shallow marine limestone lenses appear locally at the top of the Bragdon and in the lower part of the overlying Baird Formation. The brachiopods *Striatifera* and *Titanaria* indicate a Visean or Serpukhovian (Late Mississippian) age for these limestones (Watkins, 1973 ; Gordon and Dutro, 1993). The lenses reach 17 m thick and 1.2 km in length, and consist of bank and slope facies that were deposited over delta lobes (Watkins, 1993a). Deposition of the lime-

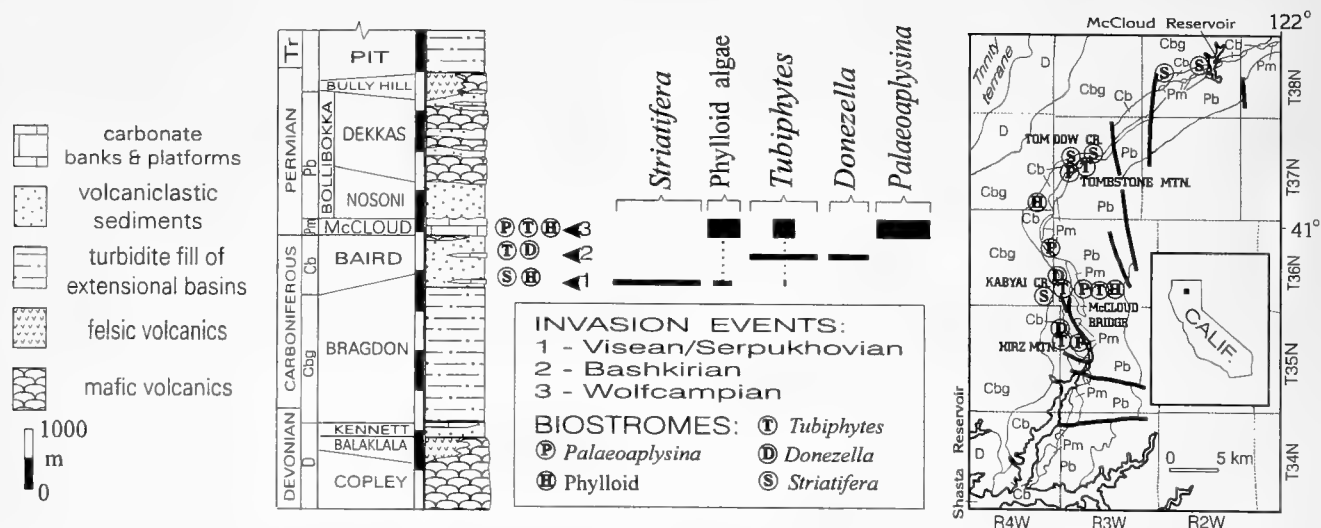


Figure 1. Occurrence of Upper Paleozoic biostromes in the eastern Klamath terrane, California; width of bars for the five taxa indicates their relative importance in biostrome formation. Detailed geologic maps of areas with biostromes are contained in Watkins (1973, 1993a, 1993b).

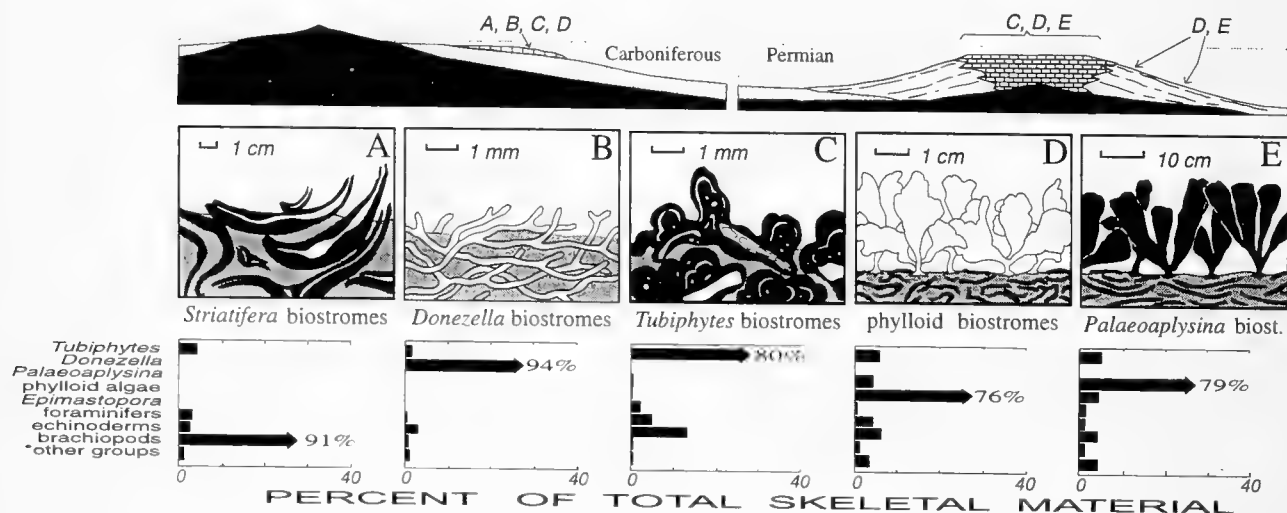


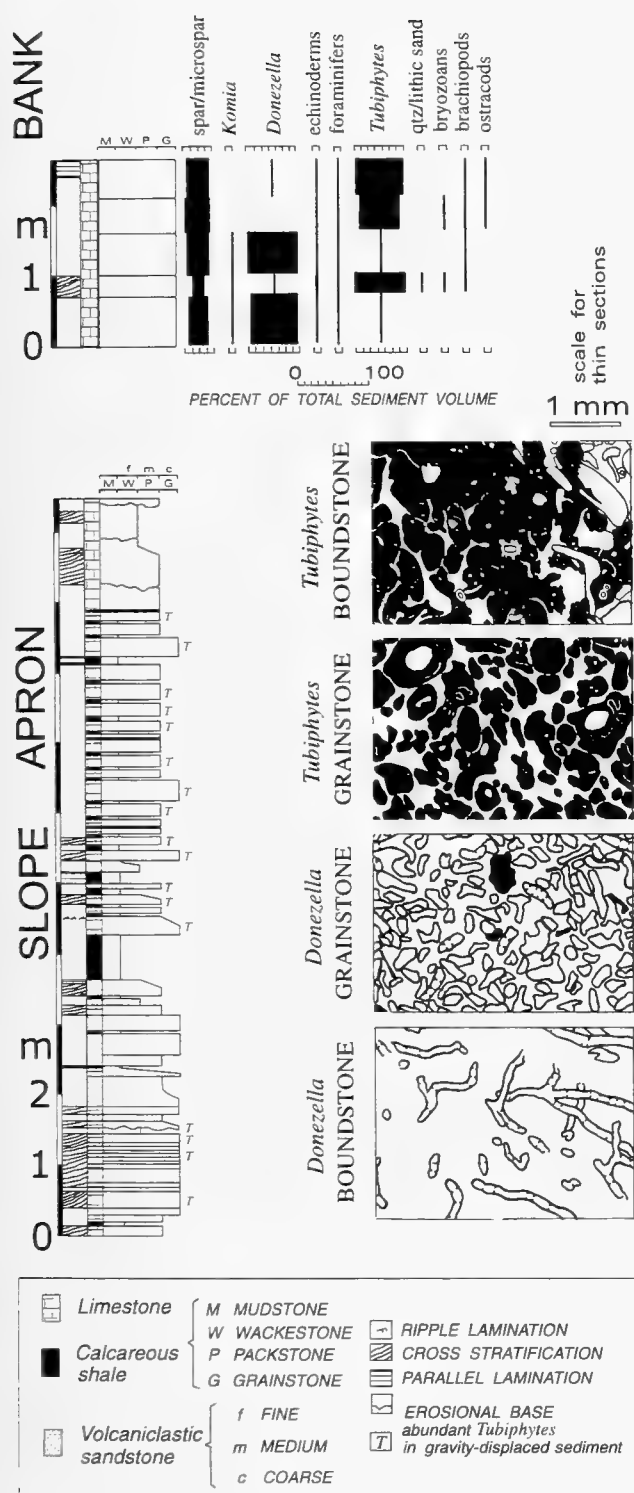
Figure 2. Environmental occurrence, life habit reconstructions, and skeletal composition of biostromes (*other groups include corals, bryozoans, annelids, molluscs, and ostracods).

stone lenses was related either to sea level rise that cut off volcaniclastic sediment supply, or to switching of active delta lobes. Carbonate deposition on deltas was short-lived and terminated by progradation of volcaniclastic sediments.

Bashkirian (Early Pennsylvanian) limestone lenses in the Baird Formation are dated by the fusulinid *Pseudostaffella* (Skinner and Wilde, 1965). The fusulinid-bearing limestones occur at Kabyai Creek (Watkins, 1973, fig. 4) and Hirz Mountain [the Hirz Mountain Limestone Member of Watkins (1973, fig. 3), who erroneously dated it as "Late Pennsylvanian or Early Permian"]. The lenses include bank and slope apron facies (Figure 3), and they reach 20 m in thickness and 2 km in breadth. In both areas, the limestone lenses are

overlain by a thick section of volcaniclastic sediments that probably ranges from Bashkirian to latest Carboniferous age.

The Baird is overlain by the Lower Permian McCloud Limestone, which contains basal Wolfcampian to early Leonardian fusulinids (Skinner and Wilde, 1965). The McCloud was deposited during an interval of volcanic quiescence as several carbonate platforms that reached tens of km in breadth (Miller, 1989; Watkins, 1990). Platforms developed over volcanic highs and grew by progradation of slope deposits and aggradation of platform-top deposits, resulting in carbonate sections over 800 m thick (Watkins, 1993b). McCloud deposition was terminated by platform subsidence and drowning in the Leonardian, and volcanism



resumed in the eKt during early Guadalupian time (Renne and Scott, 1988). Small carbonate bank deposits of Guadalupian age occur in the volcanic and volcanoclastic Bolibokka Group, but no biostromes have been reported (Stevens *et al.*, 1987; Miller, 1989).

Methods

Data on biostromes were collected as part of a sedimentologic study of Upper Paleozoic carbonates in the eKt (Watkins, 1993a, 1993b). This study involved outcrop mapping and bed-by-bed logging of five depositional lenses of Visean/Serpukhovian limestones (80 m of total section), three depositional lenses of Bashkirian limestones (142 m of total section), and one Wolfcampian slope and platform complex (901 m of total section).

In the course of this work, 81 samples were made from 60 biostromes, and 39 samples were made from beds of gravity-displaced biostromal sediment. All samples were prepared as thin sections. Compositional data were obtained as counts of 100 to 200 points per thin section, and data were pooled for samples from the same biostrome type to yield the histograms in Figure 2. Samples with larger biostrome formers were also studied as polished slabs. Twelve samples were etched in HCl to obtain silicified fossils used for measurement of species diversity.

Comparative paleoecology of biostrome and shelf-mud faunas, discussed later, uses the guild concept. Reef and biostrome guilds recognized by Fagerstrom (1987) include constructors, bafflers, binders, destroyers, and dwellers. This report follows Watkins (1993c) in subdividing the dweller guild on the basis of class-level taxonomy and functional morphology.

Biostromal deposits

Biostromes formed by *Striatifera*, phylloid algae and *Palaeoaplysina* are readily apparent in the field, but their lateral extent is difficult to determine because of brush cover. *Striatifera* biostromes have been traced for lateral distances of 45 m, and *Palaeoaplysina* and phylloid biostromes have been traced for distances of 130 m. Biostromal beds dominated by *Donezella* and *Tubiphytes*, which appear as medium-grained, relatively featureless limestone in the field, were identified by thin sections. These beds have been traced only across small roadcuts and ledges.

Striatifera biostromes

Striatifera is a linoproductid brachiopod that attached to conspecific shells with its spines, forming biostromes similar to modern mussel beds (Muir-Wood and Cooper, 1960). An undescribed species of *Striatifera*, similar to *S. striata* Fischer de Waldheim, occurs as a biostrome former in Visean/Serpukhovian limestones of the Bragdon and Baird formations.

The biostromal beds range from 40 to 110 cm thick and contain a loose framework of in-place *Striatifera*. Articulated individuals rest upon one another in a convex-downward

orientation (Figure 4A) and are attached by cementing spines. Growth asymmetry caused by crowding is common, and shells range from juveniles a few mm in size to adults 18 cm in length. These beds contain 28 to 58% *Striatifera* and 33 to 59% micrite and microspar matrix. Small encrustations of *Tubiphytes* are present on *Striatifera* (Figure 5A) and form <1 to 14% of sediment volume. Other skeletal taxa are mainly matrix-supported and scattered between the large productoids; they form <1 to 10% of sediment volume and

include crinozoans, foraminifers, small brachiopods, gastropods, corals, echinoids, and bivalves (Watkins, 1973).

Beds with in-place productoids are interbedded with erosively based packstones that contain sorted, horizontally stratified *Striatifera* valves and fragments (Figure 4B). These two lithologies, which form horizons up to 3 m thick (Figure 4C), were deposited in a moderate to high energy, bank-edge setting (Watkins, 1993a).

Donezella biostromes

Boundstone, packstone, and grainstone beds with abundant *Donezella lutugini* Maslov occur in Bashkirian limestones of the Baird Formation (Figure 3). Mamet (1991) placed *Donezella* and similar genera in the algal group Palaeosiphonocladales, but they have also been interpreted as sponges (Termier *et al.*, 1977) and possible foraminifers (Riding, 1977). Mamet *et al.* (1987) interpreted the tubules of *Donezella* as branching thalli that stood upright above the bottom and functioned as sediment baffles. However, a sediment-binding habit for donezellids is also possible (Davies and Nassichuk, 1988).

Massive beds from 35 to 120 cm thick contain 25 to 30% *Donezella* as an open-branching network of septate tubules 0.08 to 0.27 mm in diameter. The tubule network is partly contained in micrite (13–55% of sediment volume) and partly encloses spaces to 3.5 mm in size that consist of sparite (5 to 30%) and peloidal grainstone (14–25%). Fragments of echinoderms, bryozoans, foraminifers, and monaxial spicules occur in the micrite matrix, and areas of *Tubiphytes* up to 1.3 mm in size encrust *Donezella* tubules. These beds are interpreted as boundstone. Their texture and fabric are very similar to beresellid-donezellid boundstone in Bashkirian to early Moscovian reefs in the Canadian Arctic (Davies and Nassichuk, 1988).

Massive to cross-stratified beds of grainstone and packstone are 30 to 105 cm thick and contain 60 to 70% broken *Donezella* tubules (Figure 5C), 18 to 34% sparite or micrite matrix, and 1 to 8% other bioclasts, including *Komia*, *Tubiphytes*, echinoderms, foraminifers, bryozoans, brachiopods, and ostracods. Tubule fragments are 3 mm or less in length, and in some beds they show a parallel alignment of long axes. Other bioclasts, which reach 10 mm in size, are dispersed and often abraded. These beds represent sediment derived from *Donezella* boundstone, and they formed in moderate to high energy, bank and bank-edge settings.

Tubiphytes biostromes

Tubiphytes is an encruster that has been interpreted as a cyanobacterium, alga, foraminifer, sponge, or metazoan of uncertain affinity (Riding and Guo, 1992). It consists of an outer envelope of dark, fine-grained calcite and internal tubules. Senowbari-Daryan and Flügel (1993) recognized only the envelope as *Tubiphytes* and considered the internal tubules as separate, overgrown organisms. Grainstones dominated by *Tubiphytes obscurus* Maslov occur in Bashkirian limestones of the Baird Formation and Wolfcampian zones A, B and G of the McCloud Limestone (Figures 3, 6).

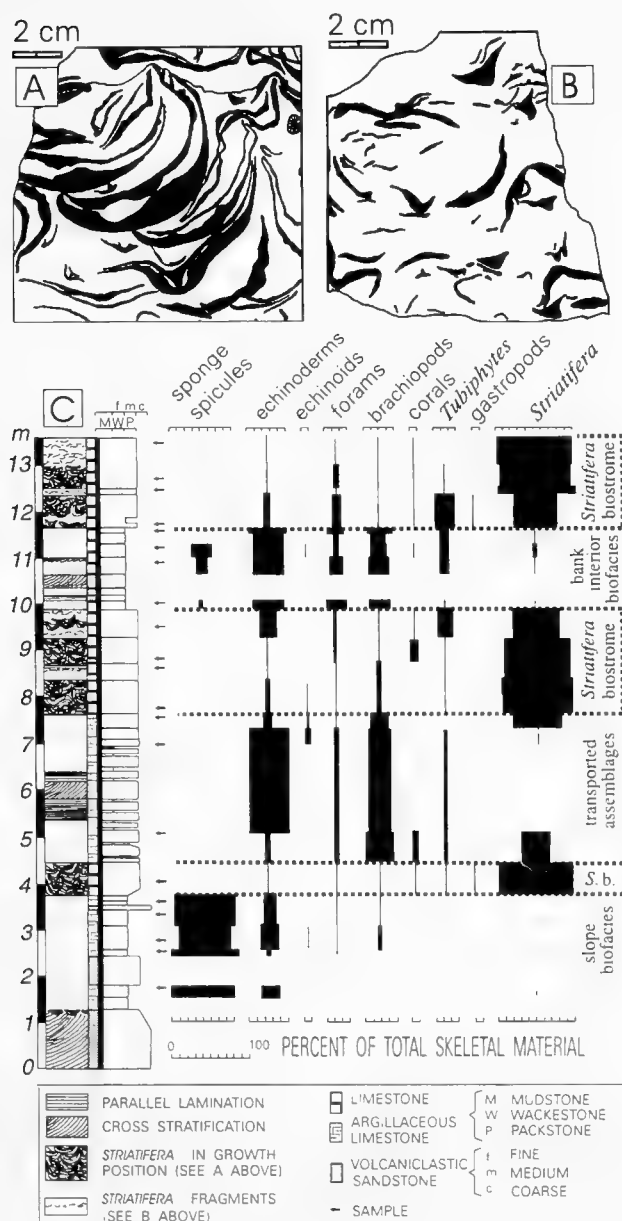


Figure 4. A. *Striatifera* in growth position. B. Rede-deposited *Striatifera* valves and fragments. C. Occurrence of *Striatifera* biostromes in limestone of the Baird Formation at Tom Dow Creek; see Watkins (1993a) for photos and location of this section.

In the bank facies of Bashkirian limestones, *Tubiphytes* grainstone forms massive to cross-stratified beds 30 to 140 cm thick. In the slope facies of these limestones, *Tubiphytes* grainstone and packstone form 10-to-30-cm-thick beds that include normal grading and small-scale cross-lamination (Figure 3). Wolfcampian *Tubiphytes* grainstone forms isolated, massive beds 0.4 to 5 m thick within platform successions of thick-bedded crinoid packstone, fusulinid packstone, and skeletal packstone (Figure 6). In Wolfcampian slope deposits at McCloud Bridge (fusulinid zone A of Skinner and Wilde, 1965), *Tubiphytes* grainstone is interbedded with limestone conglomerate and forms 10-to-60-cm-thick beds that include small-scale cross-lamination, horizontal lamination, and normal grading. At Tombstone Mountain, pebbles to small boulders of *Tubiphytes* grainstone are abundant in limestone conglomerates of fusulinid zone G.

The grainstones contain 43 to 80% *Tubiphytes* (Figure 5E) and 11 to 38% sparite to microspar matrix. *Tubiphytes* grains range from 0.3 to 1.5 mm, with a maximum size of 5 mm. Abrasion and rounding are common, particularly among smaller *Tubiphytes* grains that contain no other bioclasts. Larger *Tubiphytes* grains contain nuclei of small skeletal fragments or envelop and bind together several bioclasts. Other bioclasts, which include echinoderms, foraminifers, corals, bryozoans, brachiopods, and ostracods, reach 10 mm in size and form 1 to 19% of sediment volume. Permian beds also include the dasycladacean *Epimastopora* and indeterminate phylloid algae.

The grainstone beds indicate abundant *Tubiphytes* growth in shallow, high-energy settings where the volume of binders exceeded that of encrusted skeletal grains. Although small areas of *Tubiphytes* boundstone occur within skeletal packstone, no *Tubiphytes* bed with a complete boundstone fabric has been observed. This may indicate that *Tubiphytes* crusts were more or less continuously reworked as they formed. Kershaw (1994), in a classification of biostrome types, noted that not all biostromes consist of *in situ* skeletons. In Kershaw's classification, the *Tubiphytes* grainstone beds can be considered as "parabiostromes," which consist largely of reworked biostrome-formers, with 20% or less *in situ* material. Much of this sediment was also redeposited on slope aprons bordering bank and platform margins.

Phylloid biostromes

Phylloid algae are a morphological group of leaf-like genera that may include both red and green algae (Riding and Guo, 1991). In Late Paleozoic reefs and biostromes, their functional role included sediment baffling and voluminous production of skeletal particles (Toomey and Babcock, 1983).

Phylloid packstone occurs as two 20-cm-thick beds in a single Viséan/Serpukhovian limestone lens in the Baird Formation (Watkins, 1993a). Baird phylloids (Figure 5B) are recrystallized and generically indeterminate. In the Wolfcampian McCloud Limestone, phylloid packstone forms massive beds 0.3 to 4.5 m thick in platform successions (Figure 6). In McCloud slope deposits, gravity-displaced

phylloid packstone occurs as clasts in limestone conglomerate and thin beds with erosional bases and normal grading. Slope deposits also include less common, massive beds to 80 cm thick that represent in-place biostromes. McCloud phylloids include *Eugonophyllum* sp., but specimens in most samples are too recrystallized for identification.

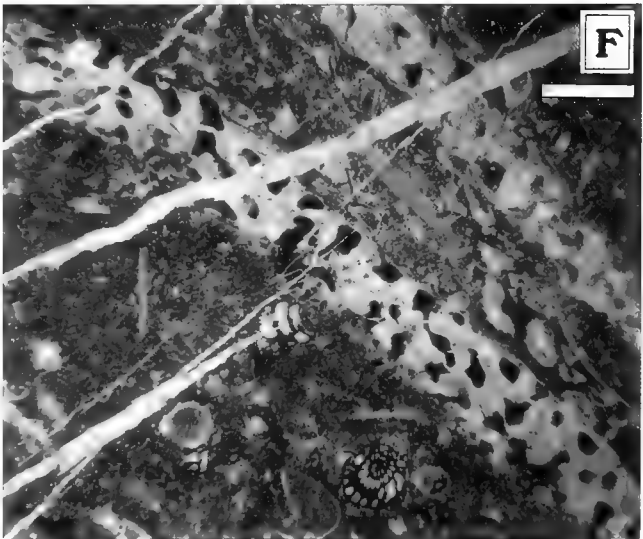
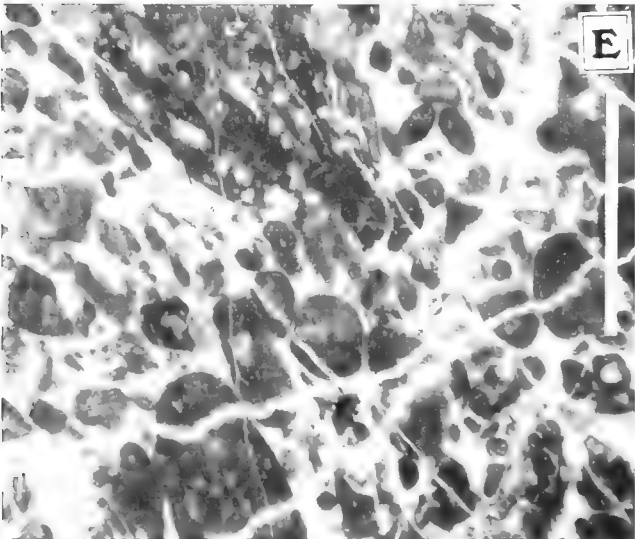
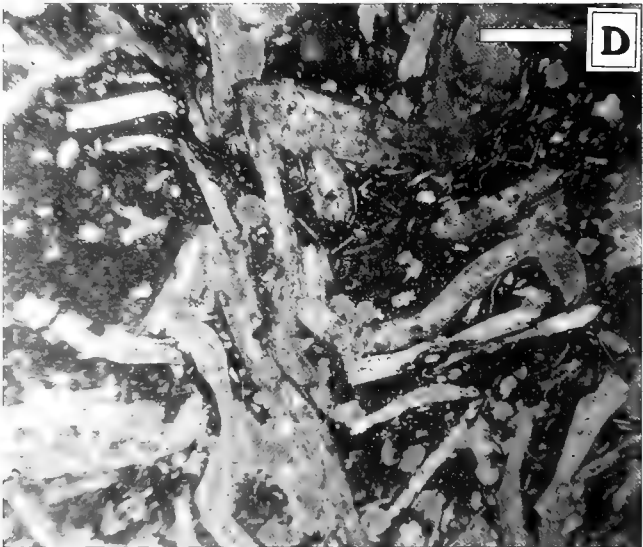
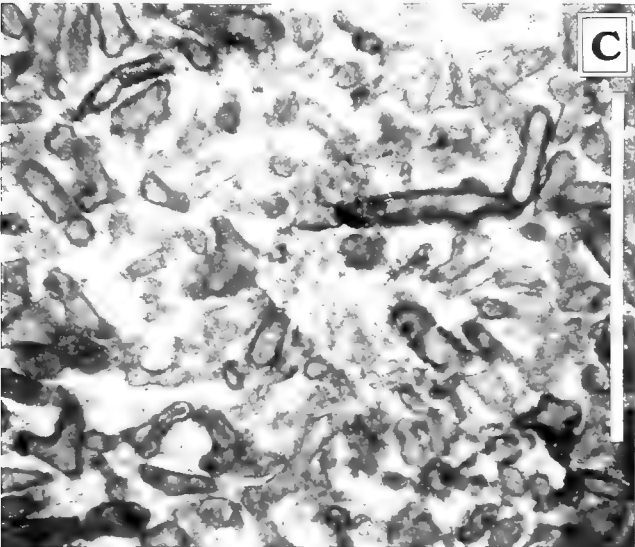
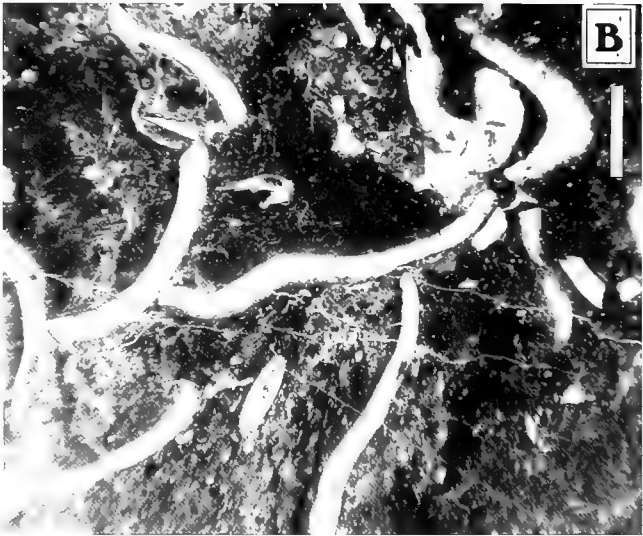
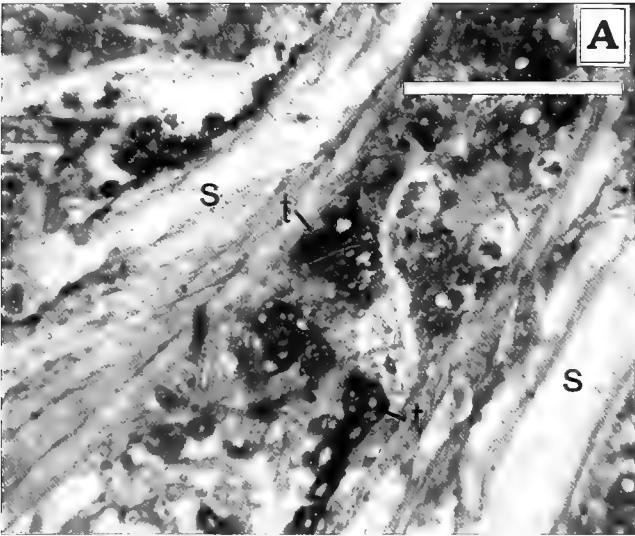
Packstones in the McCloud Limestone include 24 to 43% phylloids (Figure 5D) and 42 to 66% micrite and microspar matrix. Phylloid plates are 2 to 18 mm long, variably oriented, and closely to loosely packed. Edges of plates often appear broken but are unabraded. *Tubiphytes* forms <1 to 9% of sediment volume and occurs as loose grains and encrustations up to 4 mm long on phylloid plates. Spirorbids, fenestellid holdfasts, other bryozoans, and tetrataxiid foraminifers also encrust phylloids. Other bioclasts form 6 to 14% of sediment volume and are scattered, mostly matrix-supported, and mainly less than 5 mm in size. They include *Palaeoaplysina*, *Epimastopora*, bryozoans, foraminifers, echinoderms, gastropods, brachiopods, ostracods, and corals.

Palaeoaplysina biostromes

The enigmatic genus *Palaeoaplysina*, which consists of thin calcareous plates with an internal canal system and cellular structure, has features in common with hydrozoans, sponges, and algae (Davies and Nassichuk, 1973). *Palaeoaplysina* is an important reef and biostrome former, but its mode of life is uncertain (Beauchamp *et al.*, 1988). Breuninger (1976) inferred a binding habit for the plates, but Davies and Nassichuk (1973) and Watkins and Wilson (1989) presented evidence for an erect, frond-like growth habit.

Palaeoaplysina laminaeformis Krotov is locally common in the Wolfcampian McCloud Limestone (Figure 6). In the platform facies of the McCloud, massive beds of *Palaeoaplysina* wackestone to packstone are 0.7 to 2.2 m thick. These beds occur both as isolated units within successions of skeletal wackestones, packstones, and grainstones, and they are also interbedded with phylloid packstones as composite biostromal horizons over 4 m thick (Watkins and Wilson, 1989). McCloud slope deposits with limestone conglomerates also include common *Palaeoaplysina* beds (Watkins, 1993b). Massive *Palaeoaplysina* wackestone to packstone beds from 0.5 to 3 m thick are identical to those in the platform facies, and they are interpreted as in place biostromes of slope aprons. Less common, redeposited beds of *Palaeoaplysina* packstone are 10 to 30 cm thick and have loaded bases and ripple-laminated tops.

Beds of intergrading wackestone to packstone consist of 23 to 49% *Palaeoaplysina* (Figure 5F) and 38 to 69% micrite and microspar matrix. Plates of *Palaeoaplysina* reach 20 cm long, are mainly oriented parallel to bedding, and range from loosely to closely packed. Encrustors on *Palaeoaplysina* include *Tubiphytes*, which forms <1 to 4% of sediment volume, as well as spirorbids and bryozoans. Other bioclasts, which form 3 to 11% of sediment volume, include phylloid algae, *Epimastopora*, echinoderms, foraminifers, corals, bryozoans, brachiopods, gastropods, bivalves, and ostracods.



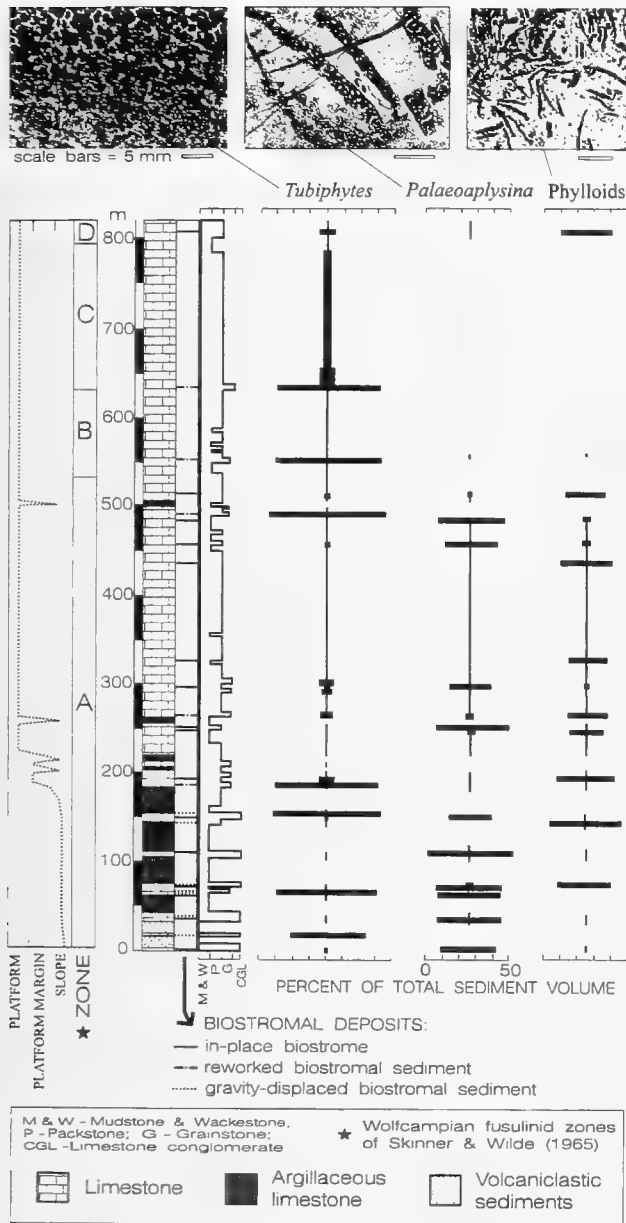


Figure 6. Biostrome occurrence in the Lower Permian McCloud Limestone at McCloud Bridge; see Watkins (1993b) for location, details of nonbiostromal lithologies, and bed-by-bed logs of parts of the section.

Biogeographic and sedimentary relations of biostrome formers

Three intervals of Late Paleozoic carbonate deposition in the eastern Klamath terrane were accompanied by bio-

strom formation. Biostromal taxa appear at or near the base of each carbonate horizon and range throughout their entire thicknesses; they have not been recorded through intervening clastic deposits. This suggests three separate invasions of the terrane by biostromal communities.

Biostromes were poorly developed during the Visean/Serpukhovian interval of carbonate deposition. The brachiopod *Striatifera* formed beds with a loose framework structure in several limestone lenses. However, *Striatifera* beds are not present in all lenses of this age (Watkins, 1993a), and their level of binding and sediment production was much less than those of other biostromes. *Striatifera* probably arrived in the eKt from the east, as it is a Tethyan genus that occurs in North Africa, Western Europe, Russia, Kazakhstan, China, and Japan (Muir-Wood and Cooper, 1960; Gordon and Dutro, 1993). Phylloid algae, which dominate two beds in one limestone lens, had only a limited role in sediment production, and their occurrence in the Baird Formation predates their Late Carboniferous rise as important producers of carbonate sediment (Chuvashov and Riding, 1984). The binder *Tubiphytes* is a minor constituent of the Visean/Serpukhovian biostromes, where its occurrence also predates its attainment of global abundance.

Bashkirian limestones of the eKt record the return of *Tubiphytes* and the appearance of *Donezella* as important biostrome formers. *Tubiphytes* grainstone forms up to 50% of the thickness of bank sections, and redeposited beds of *Tubiphytes* form up to 40% of sections deposited as slope aprons. The Bashkirian occurrence of *Tubiphytes* grainstones in the eKt corresponds to its rise in abundance during the Late Carboniferous, when it attained a cosmopolitan distribution as both a major and accessory reef and biostrome former (Chuvashov and Riding, 1984; Mamet, 1991; Senowbari-Daryan and Flugel, 1993). *Donezella* beds also form up to 50% of Bashkirian bank sections in the eKt. The Bashkirian/Moscovian was the temporal acme of *Donezella* as a sediment producer, and it forms reefs and biostromes of this age in North Africa, Eurasia, and North America (Mamet, 1991). Although phylloid algae were important and widely distributed reef and biostrome formers during the Late Carboniferous (Chuvashov and Riding, 1984; Mamet, 1991), they have not been observed in Bashkirian limestones of the Baird Formation.

Biostromes played a minor role in the construction of Wolfcampian carbonate platforms in the eKt. Beds dominated by *Tubiphytes*, phylloid algae and *Palaeoaplysina* form less than 10% of the thickness of platform sections. Lack of importance of biostromes and absence of reefs on McCloud platforms may be due to very high rates of subsidence and absence of well-defined platform margins (Watkins, 1993b). *Tubiphytes* and phylloids had a cosmopolitan distribution as important reef and biostrome formers in the Early Permian (Chuvashov and Riding, 1984; Riding and Guo, 1991; Senowbari-Daryan and Flugel, 1993). *Palaeo-*

Figure 5. A. Detail of *Striatifera* bed showing small encrustations of *Tubiphytes* (t) on *Striatifera* valves (s), Baird Formation, Tom Dow Creek. B. Phylloid packstone, Baird Formation, North Fork. C. *Donezella* grainstone, Baird Formation, Kabyai Creek. D. Phylloid packstone, McCloud Limestone, McCloud Bridge. E. *Tubiphytes* grainstone, McCloud Limestone, Tombstone Mountain. F. *Palaeoaplysina* packstone, McCloud Limestone, McCloud Bridge. All scale bars are 2 mm.

aplysina first appears in the Middle Pennsylvanian of Utah, and by the Wolfcampian it is present as a major reef and biostrome former in a belt around the northern margin of Laurentia, including occurrences in Idaho, British Columbia, the Canadian Arctic, Svalbard, and the Urals (Ritter and Morris, 1997). *Palaeoaplysina* is also known from the Akiyoshi terrane of Japan (Machiyama, 1991).

Early Permian *Palaeoaplysina* buildups appear to have had a relatively wide environmental range, occurring in the Canadian Arctic from inner shelf to upper slope settings (Beauchamp *et al.*, 1988). This relation is also evident in the McCloud Limestone, where *Palaeoaplysina* biostromes are present in both platform and slope deposits. McCloud slope deposits consist of alternations of thin-bedded argillaceous limestones and horizons with limestone conglomerates (Figure 6). *Palaeoaplysina* biostromes form 15 to 45% of the thickness of conglomeratic horizons. Occurrence of *Palaeoaplysina* biostromes on tops of conglomerates, as well as on volcanoclastic breccia at the very base of the McCloud Limestone (Watkins, 1993b, fig. 4), suggest a role as a pioneer community among carbonate sediment producers.

Comparison of biostromes and shelf-mud biofacies

Paleoecological aspects of the biostromes can be best understood by comparison with contemporaneous shelf-mud biofacies of the eKt (Figure 7). The shelf biofacies occur in bioturbated, clastic and carbonate muds of Viséan/Serpukhovian to early Guadalupian age (Coogan, 1960; Watkins, 1973; Yancey and Hanger, 1985). Echinoderms (mainly crinoids) form 50–70% of skeletal material in these biofacies, followed by brachiopods (4–36%), bryozoans (3–13%), foraminifers (1–11%), and molluscs, corals, and minor groups (<1–10%). Four bivalve guilds, three bryozoan guilds, two

brachiopod guilds, and a gastropod "superguild" include most of their macrofaunal species. Species data for echinoderms, which occur as disarticulated ossicles, are not available.

In contrast, all five types of biostromes are dominated by a single binding, baffling, or framebuilding species that forms over 70% of skeletal material (Figure 2). Although several such species may cooccur within a biostrome, only one predominates. For example, *Tubiphytes*, phylloids, and *Palaeoaplysina* commonly occur together in Lower Permian beds, but in each case one of these taxa is clearly dominant (Figure 6). Dweller guilds generally form 20% or less of skeletal material in beds, and their composition is similar in all five types of biostromes. Crinozoans and foraminifers are the most common dweller taxa (Figure 2), and small amounts of skeletal material (usually 2% or less each, except for *Striatifera* biostromes) are represented by brachiopods, bryozoans, molluscs, corals, annelids, and ostracods.

Bulk collections of silicified specimens from *Striatifera* and phylloid biostromes permit a more detailed consideration of dweller taxa (foraminifers, ostracods, and echinoderms have not been studied and are not included in this discussion or in plots of species diversity in Figures 7 and 8). The most diverse groups among dweller taxa are brachiopods and gastropods, followed in decreasing order by bryozoans, bivalves, corals, rostroconchs, and annelids. The composition and species diversity of dweller taxa in the biostromes is nearly identical to that in carbonate shelf-mud biofacies of Bashkirian and Wolfcampian age (Figure 7). In the Wolfcampian, the same species occur in shelf-mud biofacies, phylloid biostromes, and *Palaeoaplysina* biostromes (Watkins and Wilson, 1989). These relations suggest that most dweller taxa in the biostromes were not specialized for these habitats, but were immigrants from level-bottom, carbonate

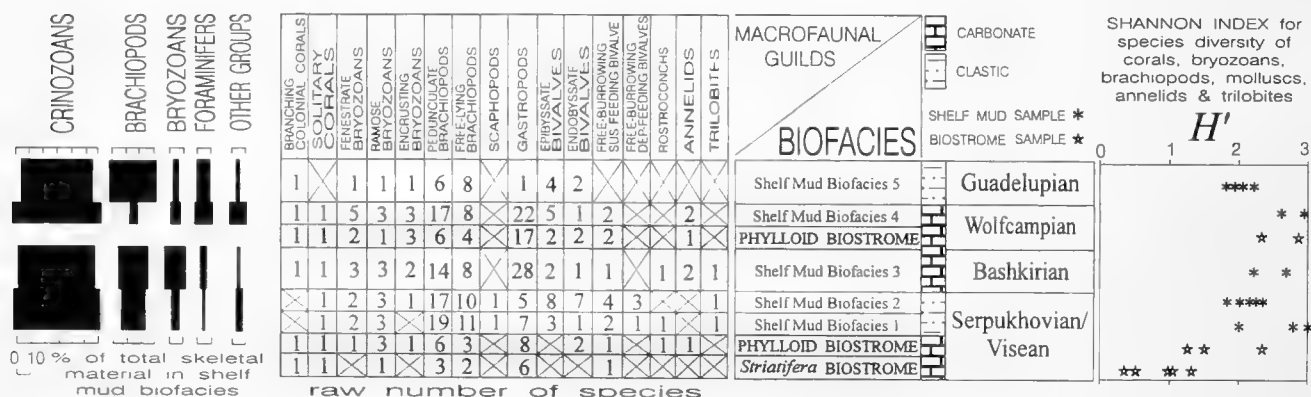


Figure 7. Faunal comparison of Upper Paleozoic biostromes and shelf mud biofacies of the eastern Klamath terrane. Biofacies are arranged vertically by four intervals of time, but this plot is not a stratigraphic section. For the Serpukhovian/Viséan, relative stratigraphic position of phylloid and *Striatifera* biostromes is not known, and both overlap in stratigraphic range with shelf-mud biofacies. For the Wolfcampian, plotting of the phylloid biostrome below the shelf-mud biofacies is arbitrary, as these biotas are interbedded. Shelf-mud biofacies and number of specimens in samples (*n*) are as follows: 1-*Dorsoscyphus* association, Bragdon Formation, *n* = 442; 2-*Rugosochonetes* association, Baird Formation, *n* = 1203; 3-*Lissomarginifera* association, Hirz Mountain Limestone Member of Baird Formation, *n* = 1734; 4-*Crurithyris* (= *Cruricella*) association, McCloud Limestone, *n* = 1663; 5-*Anidanthus-Spiriferella* faunule, *n* = 435. Sample sizes for biostromes are as follows: Wolfcampian phylloid, *n* = 472; Serpukhovian/Viséan phylloid, *n* = 2496; *Striatifera*, *n* = 1261.

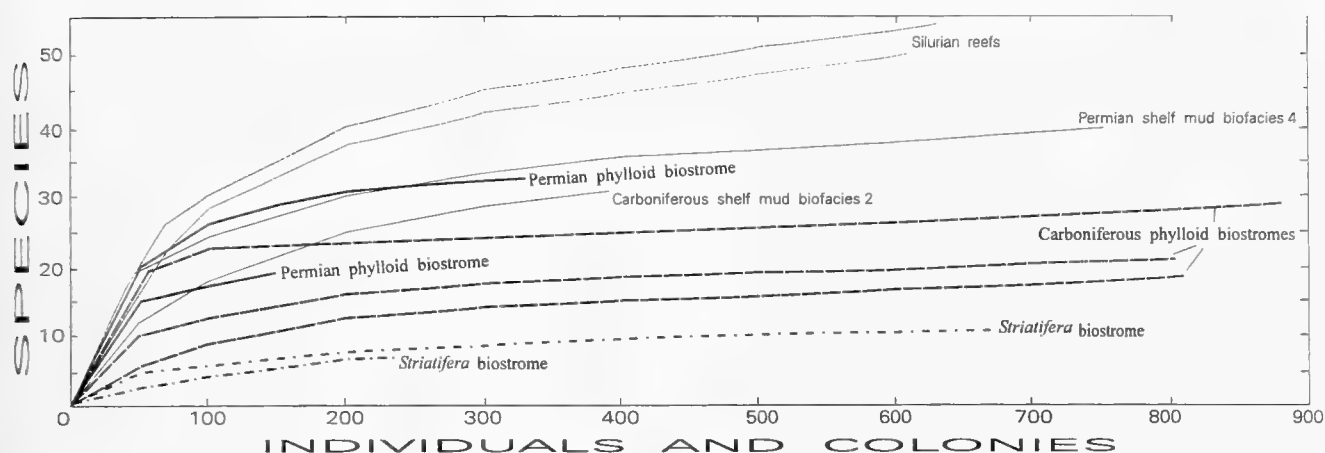


Figure 8. Rarefaction curves for Upper Paleozoic biostromes and shelf-mud biofacies of the eastern Klamath terrane. Also shown for comparison are two samples from Silurian reefs (Watkins, 1996). Data are for corals, bryozoans, brachiopods, molluscs, annelids and trilobites.

mud environments.

Trends in species diversity

Following the Late Devonian extinctions, the global number of marine families increased rapidly, reaching a stable level near the end of the Early Carboniferous that was maintained for the rest of the Paleozoic (Sepkoski, 1992). This pattern of Late Paleozoic stasis is also shown by species diversity of Viséan/Serpukhovian to early Guadalupian shelf-mud biofacies of the eKt, as measured by H' and rarefaction (Figures 7, 8). Reef biotas were much slower to recover from the Late Devonian extinctions, and complex reef communities were not reestablished until the Middle Permian (Sheehan, 1985; Copper, 1988). This slow recovery is also suggested by species diversity data from Upper Paleozoic biostromes in the eKt. Average species-diversity in eKt Carboniferous biostromes is less than that of shelf-mud biofacies. Species diversity in phylloid biostromes increased by the Early Permian, when they attained a diversity equivalent to that of carbonate shelf-mud biofacies (Figures 7, 8). Even so, diversity of the Early Permian biostromes did not reach the levels of reefs that existed before the Late Devonian extinctions, as shown by rarefaction curves for Silurian reefs (Figure 8).

Conclusions

Three intervals of Late Paleozoic volcanic quiescence and carbonate deposition in the eastern Klamath terrane were accompanied by development of biostromal communities. Except for loosely cemented productoid brachiopods, framebuilders are absent, and bafflers and binders of algal or problematic affinity are the dominant biostrome formers. Stratigraphic ranges and peaks in abundance of eKt biostromal taxa are like their occurrences elsewhere. Biostrome formers include a mixture of cosmopolitan, Tethyan and Laurentian affinities. An increase in species diversity from

Early Carboniferous to Early Permian biostromes in the eKt probably reflects global recovery of reef biotas following the Late Devonian extinctions.

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The turrilitid ammonoid *Mariella* from Hokkaido — Part 2 (Studies of the Cretaceous ammonites from Hokkaido and Sakhalin — LXXXVI)

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Abstract. The following five taxa of the genus *Mariella* of the Turrilitidae from the Upper Albian and Lower Cenomanian of Hokkaido are described: (1) *M. (Mariella) bergeri* (Brongniart, 1822), (2) *M. (M.) aff. bergeri* (Brongniart), (3) *M. (M.) miliaris* (Pictet and Campiche, 1861), (4) *M. (M.) cf. carrancoi* (Böse, 1923) and (5) *M. (M.) gallienii* (Boule, Lemoine and Thévenin, 1907). The present study gives new or revised information as to the taxonomy and stratigraphic occurrences of these species.

Key words: Late Albian early Cenomanian, *Mariella (Mariella) bergeri*, *M. (M.) carrancoi*, *M. (M.) gallienii*, *M. (M.) miliaris*

Introduction

In Part 1 Matsumoto *et al.* (1999) described three well defined species of *Mariella* from the Lower Cenomanian of the Soeushinai area (northwestern Hokkaido). In Part 2 we continue to describe some more species (five taxa) from the Upper Albian and Lower Cenomanian of Hokkaido. The material is mostly from the Soeushinai area, except for a supplementary specimen from the Shuparo [=Shuyubari] area of the Yubari Mountains (central Hokkaido).

With respect to the location and stratigraphic assignment of the material from the Soeushinai area, readers may refer to the route maps in the two papers by Nishida *et al.* (1996, figs. 3–5; 1997, fig. 11) and for more information to the locality guide and maps given by Matsumoto and Nishida (1999, figs. 6, 7) as an Appendix to Part 1. The locality in the Shuparo area will be identified more specifically in the description of the species concerned.

The following symbols are used for the repositories of the specimens described in this paper.

GK: Type room, Department of Earth and Planetary Sciences, Kyushu University, Fukuoka

GS: Geological Collections, Faculty of Culture and Education, Saga University, Saga

Palaeontological descriptions

(Continued from Part 1)

Mariella (Mariella) bergeri (Brongniart, 1822)

Figure 1

Turrilites bergeri Brongniart, 1822, p. 395, pl. 7, fig. 3.

Mariella bergeri (Brongniart). Spath, 1937, p. 510, pl. 57, fig. 28; text-fig. 178; Drushchits, 1960, p. 266, pl. 12, figs. 2, 3; Seyed-Emami, 1982, p. 419, pl. 7, figs. 11, 12.

Mariella (Mariella) bergeri (Brongniart). Chiriac, 1960, p. 6, pl. 1, figs. 10, 11; Klinger and Kennedy, 1978, p. 28, text-fig. 6E (only); Atabekian, 1985, p. 27, pl. 2, figs. 4, 5; pl. 3, figs. 1–11; pl. 4, figs. 1–7; Kennedy, 1996, in Gale *et al.*, p. 583, figs. 160, 28a, b, i, j, l, o, p; 29h, i, m.

Paraturrilites (Bergericeras) bergeri (Brongniart). Wiedmann and Dieni, 1968, p. 80, pl. 7, fig. 5; pl. 9, figs. 2, 5.

Turrilites (Bergericeras) bergeri bergeri (Brongniart). Scholz, 1979, p. 40, pl. 8, figs. 12, 14, 15, 17.

Holotype.—The original of *Turrilites bergeri* Brongniart, 1822, pl. 7, fig. 3 (by monotypy).

Material.—GS. G183 (Figure 1–1, 2) collected by Y.K. on 25 September 1995 at loc. R803 and GS. G184 (Figure 1–3) collected by Y.K. and others on 15 August 1996 at loc. R813, both in situ from the upper part of the Member My2, (mudstone with frequently intercalated laminae and beds of sandstone), well exposed on the floor of the Sounnai River (for its location see fig. 6 in Part 1); GK. H8512, a small specimen collected by Jun Aizawa and T.M. on 14 August 1998 at loc. R8005 (close to R803) from a lenticular layer of sandstone in the Member My2.

Description.—Each of the three specimens is a fragmentary whorl of half ammonoid preservation. They can be regarded as representing whorls of roughly successive growth stages. The small, unillustrated GK. H8512 preserves shelly matter, showing small tubercles in four rows at



Figure 1. *Mariella (Mariella) bergeri* (Brongniart). 1. GS. G183, slightly oblique, lateral view showing the sedimentary structure of the host rock in the left part, $\times 1$. 2. GS. G183, upside-down lateral view, showing the whole part of the preserved flank, $\times 1.2$. 3. GS. G184, upside-down lateral view, $\times 1$. (Photos by N. Egashira without whitening.)

subequal intervals. The tubercles are connected by weak ribs.

GS. G183, about 22 mm in height, is somewhat deformed. It shows three rows of transversely elongated tubercles at equal intervals on the flank. The tubercles are aligned obliquely on weak ribs. Eleven tubercles are counted on the exposed part of the flank, showing ornamentation of moderate density. There is an extra tubercle in the upper row, but it is finer and its upwardly extended rib is faint (see the upper left part of Figure 1-1 or the lower right part of Figure 1-2). As the specimen is an abraded internal mould, the tubercles are not pointed. The tubercles of the fourth row are not exposed on the flank.

GS. G184 is comparatively large, 32 mm in whorl height

and 65 mm in diameter. It is in a nodule and slightly deformed. Shell material is preserved for the most part. The exposed whorl face is subrounded, with a broadly convex main flank and a well rounded upper shoulder. The tubercles are in four rows. They are uniformly spinose and conical at their base. The three rows on the main flank are equidistant; the fourth row is closer to the third at the base. The heads of the spines are, however, nearly equidistant, since the first spine extends obliquely upward, the second laterally, the third slightly downward and the fourth vertically downward (see Figure 1-3, in which the whorl is set upside down). The tubercles are connected transversely by low ribs in somewhat oblique orientation and those of the first row extend upward to the ribs. Some of the ribs appear to be doubled between the tubercles of adjacent rows.

Comparison.—The small specimen (GK. H8512) is comparable with a young specimen illustrated by Atabekian (1985, pl. 3, fig. 1). The second specimen (GS. G183) is comparable with a middle-aged whorl of a figured example (e.g., Atabekian, 1985, pl. 4, fig. 6). The third specimen (GS. G184) is roughly as large as the preserved last whorl of such examples as figured by Scholz (1979, pl. 8, figs. 12, 14, 15), but the uniform spinosity of its ornamentation seems to be peculiar. It should be noted, however, that on a portion of this specimen where the shell layer is stripped off, there are no spines and the tubercles are expressed as transversely elongated elevations like those of GS. G183.

Judging from the above observations, the described specimens can be identified with *M. (M.) bergeri*, although they are incomplete.

Occurrence.—As for material. The upper part of the Member My2 is regarded as the uppermost Albian (Nishida *et al.*, 1996, p. 93; Matsumoto and Nishida, 1999, p. 116).

Discussion.—Klinger and Kennedy (1978, p. 28, pl. 7, figs. C, D; text-fig. 7A) have recorded *M. (M.) cf. bergeri* from the "Lower Cenomanian I" of Zululand (South Africa). It shows a lower apical angle and its lower three rows of tubercles are according to those authors equidistant. It is possibly an example of *M. (M.) dorsetensis* (Spath) from South Africa, whereas "*M. (M.) dorsetensis*" of Klinger and Kennedy (1978, p. 31, pl. 7, fig. F; text-figs. 3A, 8A) is certainly *M. (M.) lewesiensis* (Spath).

Mariella (Mariella) acanthotuberculata Klinger and Kennedy (1978, p. 30, pl. 7, figs. C, D; text-fig. 7A), from the "Lower Cenomanian II" of Zululand, has spinose tubercles in four rows on every whorl, but its ribs and tubercles are relatively coarser and less numerous than those of our specimen (GS. G184). Moreover, it shows a higher apical angle (50° – 60°) and it is different in whorl shape from any example of *M. (M.) bergeri*, for its whorls show a quadrate section and a much lower ratio of height to diameter. Incidentally, the described specimens of *M. (M.) acanthotuberculata* are tiny but beautifully preserved. Here again the spinosity is finely shown when the shell is well preserved.

Mariella (Mariella) aff. bergeri (Brongniart, 1822)

Figures 2; 3-1

Material.—A single specimen, GS. G185 (Figure 2), collected by Y.K. on 29 June 1992 from one of the boulders (p4) at loc. R520 of the East Suribachi-zawa (for the location see Matsumoto and Nishida, 1999, fig. 6). It was probably derived from the basal part of the Member My3. *Graysonites adkinsi* Young was obtained from another boulder at R520.

Description.—Shell is of moderate size, about 140 mm in tower height (total whorl height, including the inferred missing portion) and 55 mm in diameter of the last septate whorl. The rate of size increase between successive whorls is moderate, maintaining a value of 1.37. The apical angle is estimated at 42°. The ratio between whorl height and diameter in the septate stage is constant at 0.43 (see Table 1).

The exposed part of the whorl face is rounded in gross view. In more detail, a nearly flat but narrow space is recognized in the uppermost part of the whorl face. This slopes down gradually to the convex main flank, which then

slopes down inward toward the lower whorl seam. The whorl junction is thus deep and well marked. The siphuncle runs along the midline of the uppermost flat belt.

Despite the regular shell shape in the septate stage, the last part (*i.e.*, the body chamber) of this specimen is much distorted and curved upward. This aberrant shape is similar to that in certain species of *Eubostrychoceras* Matsumoto, 1967. However, whether it is an original character or a product of secondary deformation cannot be decided from this single specimen.

There are three rows of tubercles on the exposed whorl face. The first row is somewhat above the middle of the flank, the second row is well below the midline and closer to the third row, which in turn runs slightly above or nearly along the lower whorl seam. These three rows tend to shift downward with growth. The tubercles of the fourth row are not observable from the outside. They probably lie on the unexposed lower whorl face. The tubercles increase in number with growth, from 24 in the preserved young whorl to 34 in the last septate whorl. Those of the two rows on the main flank are moderately coarse and strengthen with growth. The tubercles in the first row extend upward to

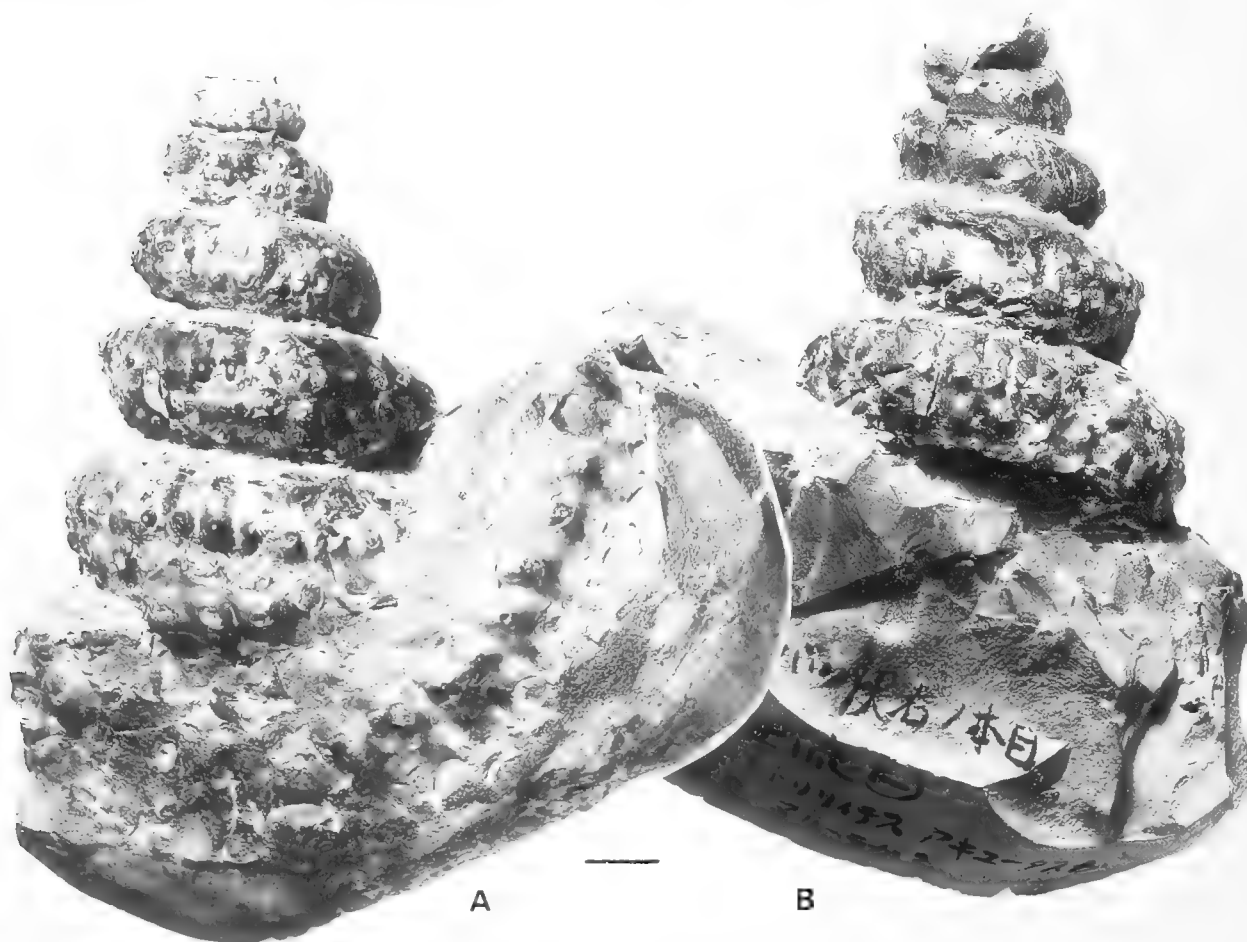


Figure 2. *Mariella (Mariella) aff. bergeri* (Brongniart). GS. G185, two lateral views, in which A is turned 180° to B, $\times 1$. (Photos by N. Egashira without whitening.)

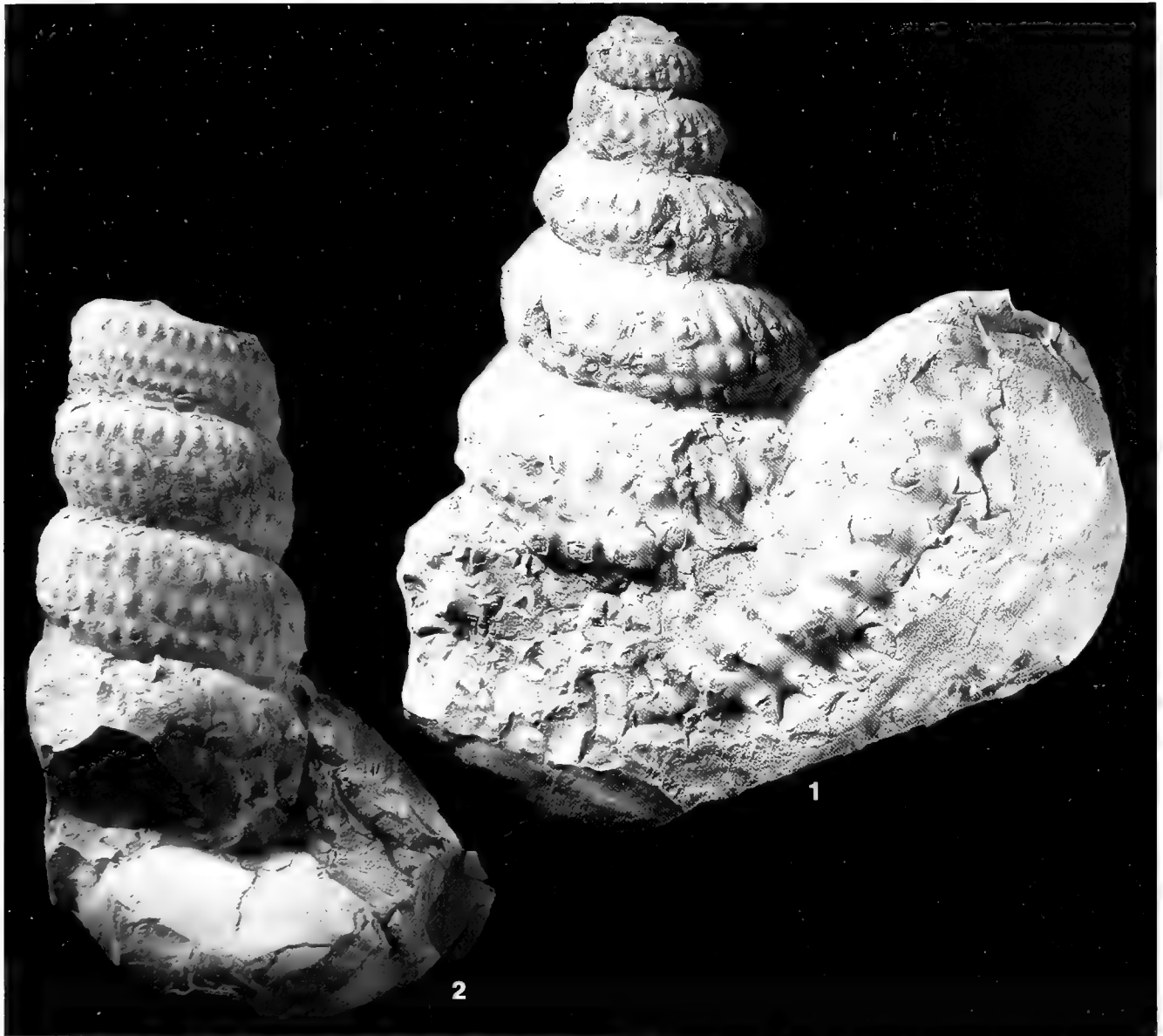


Figure 3. 1. *Mariella (Mariella) aff. bergeri* (Brongniart). GS. G185, lateral view, $\times 1.1$. 2. *Mariella (Mariella) miliaris* (Pictet and Campiche). GS. G186, lateral view, $\times 1.1$. (Photos by N. Egashira with whitening.)

form distinct ribs which fade away onto the uppermost flat belt. The tubercles of the second row are conical and become slightly larger than those of the first row with growth. On the body chamber the tubercles of these two rows strengthen and become spinose. The spines of the tubercles in the second row are much elongated and sharply pointed terminally.

The suture is observable here and there, although it is not traced completely.

Measurements. See Table 1.

Comparison.—In gross view the septate part of this specimen is similar to some specimens of *Mariella (Mariella) bergeri* (see list of synonymy in the preceding species). The apical

Table 1. Measurements of *Mariella (Mariella) aff. bergeri* (Brongniart). Measured specimen: GS. G185 (Figure 2).

| Whorl (Order)* | 1st | 2nd | 3rd | 4th | 5th |
|---------------------|------|------|------|------|------|
| Diameter (in mm) | 16.5 | 25.5 | 35.0 | 48.0 | 65.0 |
| Height (in mm) | 7.5 | 11.0 | 15.0 | 20.0 | 28.0 |
| Height/Diameter | .45 | .43 | .43 | .42 | .43 |
| Tubercles per whorl | 24 | 26 | 28 | 30 | 33 |

* The 1st, 2nd, 3rd etc, on the line "Whorl" indicate the descending order of the whorl (= in an adapertural direction) within the preserved part of the specimen.

angle of the former is certainly larger than the average of the latter, but it can be placed at the extreme end of the wide range of variation in the latter. The existence of a flat belt in the uppermost part of the exposed whorl face seems to be particular to this specimen, although the belt is narrow.

The increase in the number of tubercles or ribs per whorl with growth from 24 in youth to 34 in the last septate stage may be characteristic of this taxon. This rib density is between that of *M. (M.) bergeri* and of *M. (M.) miliaris* (*vide infra*), but the ribs and tubercles are not so fine as those of *M. (M.) miliaris*, becoming rather coarser with growth. The strong tubercles on the flank in the adult whorl have prominent spines. This is another diagnostic feature of this specimen. If the ascending feature of the last part of the body chamber were an original character, it could be regarded as another diagnostic feature, but this should be confirmed by additional material.

To sum up, this specimen probably represents an early Cenomanian new species which was derived from typical *M. (M.) bergeri* of late Albian age. As only a single specimen from a boulder nodule is available, it would be better to call it provisionally *Mariella* (*M.*) *aff. bergeri* (Brongniart).

Occurrence.—As for material.

Discussion.—*Turrilites spinosus* Kossmat (1895, p. 142, pl. 20, fig. 3) [= *Turrilites brazoensis* of Stoliczka, 1866, p. 189, pl. 88, fig. 3, (*non* Roemer, 1852)], from the lower Utatur Group of South India, has four rows of spinose tubercles. The original specimen is a large fragmentary whorl (probably body chamber) on which ribs are often bifurcated at the tubercle and some riblets are irregularly added. Certainly it has no affinity with the present taxon. It might be a *Pseud-helicoceras*, as Breistroffer (1947, p. 44) suggested.

***Mariella* (*Mariella*) *miliaris* (Pictet and Campiche, 1861)**

Figures 3-2; 4-1, 2

Turrilites bergeri Brongniart var. *miliaris* Pictet and Campiche, 1861, p. 136; 1862, pl. 58, fig. 5.

Mariella miliaris (Pictet and Campiche). Spath, 1937, p. 514, pl. 57, figs. 25, 26, text-fig. 179.

Mariella (*Mariella*) *miliaris* (Pictet and Campiche). Chiriac, 1960, p. 456, pl. 1, figs. 14-16; pl. 2, figs. 17-20; Renz, 1968, p. 88, pl. 18, fig. 10; text-figs. 31m, 32h; Förster, 1975, p. 189, pl. 7, figs. 6; Klinger and Kennedy, 1978, p. 29, pl. 3, fig. J, text-fig. 3E; Atabekian, 1985, p. 29, pl. 5, figs. 5-12, pl. 6, figs. 1-3; Wright and Kennedy, 1996, p. 333, pl. 100, fig. 28.

Turrilites (*Bergericeras*) *bergeri bergeri* Brongniart. Scholz, 1979, p. 40 (pars), pl. 9, fig. 1 only.

Holotype.—The original of Pictet and Campiche, 1861, p. 136; 1862, pl. 58, fig. 5 (reillustrated by Renz, 1968, pl. 18, fig. 10) (by monotypy).

Material.—GS. G186 (Figures 3-2 and 4-1), obtained by Y.K. on 16 August 1982 from a transported nodule at loc. R575 of the Suribachi-zawa, probably derived from the Member My3. GS. G187 (half ammonoid preservation) found by Y.K. on 31 July 1997 in a transported nodule at loc. R967 (for the location see Nishida *et al.*, 1997, fig. 11) on the upper course of the River Kotanbetsu within the outcropping area of the Member My5. GS. G188 (Figure 4-2) (half ammonoid preser-

vation) obtained by Y.K. on 18 October 1993 from a nodule in the second northern branch rivulet of the Kita-no-sawa, a tributary of the River Shuparo in the Yubari Mountains. It is inferred to have been derived from one of the Members Mc to Me of Kawabe *et al.* (1996, p. 449, fig. 4-3). These members correspond to units llc and lld of Matsumoto (1942) and are referred to the lower part of the Cenomanian.

Description.—The three specimens are moderately large. They preserve several whorls. GS. G186 consists of four slightly distorted whorls with a low ratio of increase in diameter. Hence, the apical angle appears to be acute, although whorls of earlier growth stages are not preserved. In the two other specimens of middle to late growth stages, the ratio of increase in diameter is slightly larger than the above and the estimated apical angle would be about 25°, provided that their original total whorl height (= tower height) was about 200 mm.

The exposed whorl face is semielliptical, although the main part of the flank is less convex in GS. G186 in comparison with the two others. The contact between whorls is moderate, showing an impressed junction.

Tubercles in four rows are moderately crowded and numerous, 36 per whorl in GS. G186 and 17 or 18 to half a whorl in GS. G188. They are disposed regularly; those of the first row are placed some way above midflank and extend upward to the ribs which reach the upper whorl seam with decreasing intensity. The conical tubercles of the second row lie below midflank. The tubercles of the third row are somewhat smaller than the above and appear to be granular. The tubercles of the fourth row lie in the inter-whorl junction. They may be somewhat clavate. The tubercles of the three rows on the flank are disposed on an adapturally displaced line, i.e., an approximate extension of the upper rib. The interval of the three rows on the flank slightly decreases downward. The fourth tubercle lies close to the third and the rib is bent at the lower whorl seam, running on the lower whorl surface with a gentle curvature toward the umbilicus.

The suture is only partly exposed and hardly traced wholly.

Measurements.—See Table 2.

Comparison.—The holotype of this species is a piece of a whorl as shown by a photographic illustration of Renz (1968, pl. 18, fig. 10). It was distinguished as a variety from typical "*Turrilites bergeri*" by finer and denser ornament. Although *M. miliaris* was raised to the status of an independent species by Spath (1937, p. 514), the available material was not ample. More material was added by subsequent authors, especially by Chiriac (1960) from Eastern Europe and by Atabekian (1985) from Western Asia. Thus, it has become clear with time that this species shows a considerable extent of variation in morphological characters.

The number of tubercles (or ribs) in each row is around 36 in our specimens. This is within the range of variation from 33 to 40 in the material of Atabekian (1985, p. 29). The apical angle is recorded as 42° in a British specimen (Wright and Kennedy, 1996, p. 333), whereas it is 35°, 30° and even 25° in some specimens from Western Asia (Atabekian, 1985, p. 29). In this respect the described specimens from Hokkaido can be regarded as examples with a comparatively

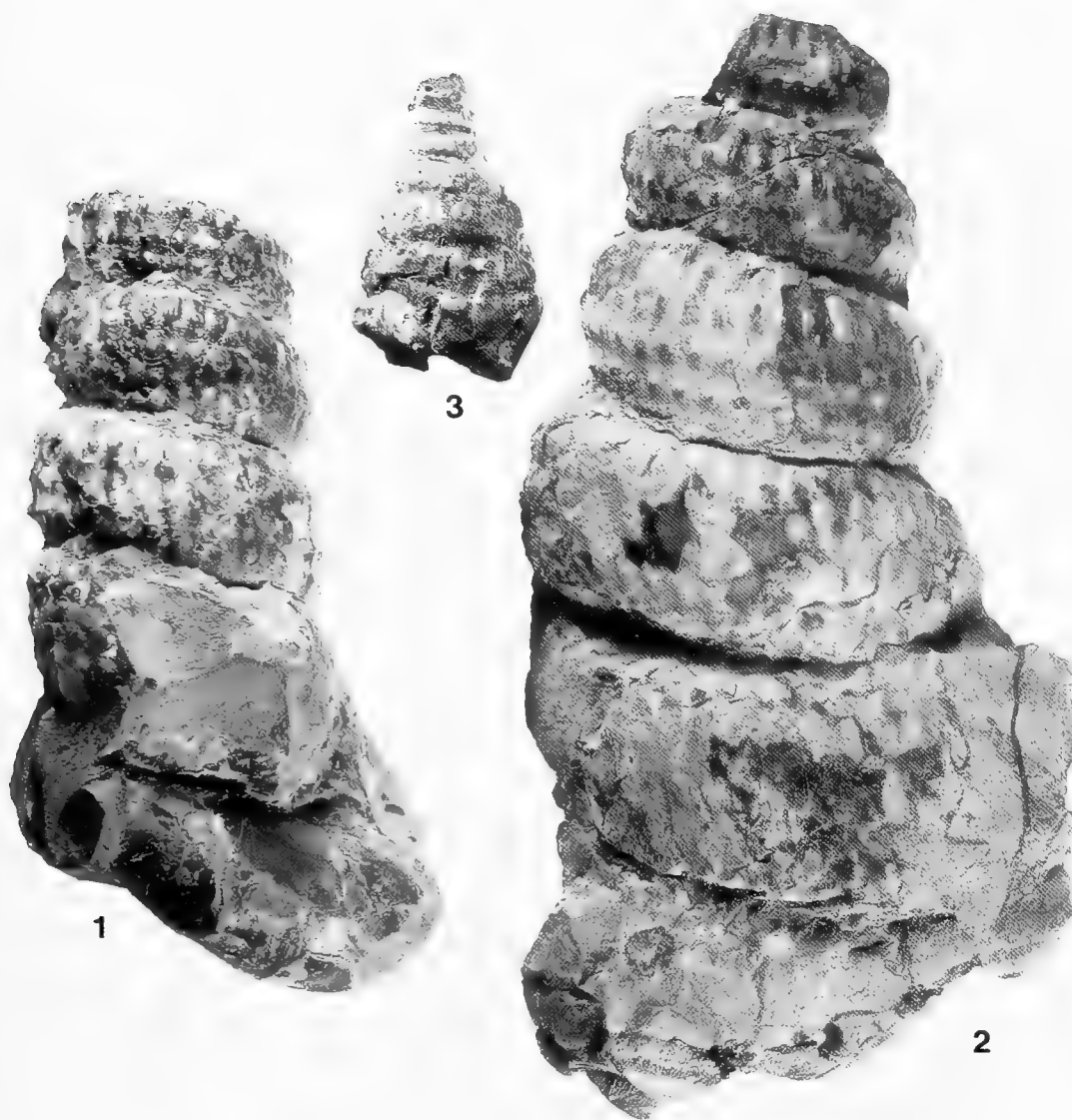


Figure 4. 1, 2. *Mariella (Mariella) miliaris* (Pictet and Campiche). 1. GS. G186, lateral view (90° anticlockwise turned from the view of Figure 3-2), $\times 1$. 2. GS. G188, lateral view, $\times 1$. 3. *Mariella (Mariella)* cf. *carrancoi* (Böse). GK. H8507, lateral view, $\times 1.5$. (Photos by N. Egashira without whitening.)

smaller apical angle within the range of this species.

Hitherto described specimens of this species from various regions of the world are rather small. Most of them are not adult. In fact, the two specimens figured by Atabekian (1985, pl. 5, fig. 5; pl. 6, fig. 1) appear to exemplify whorls of younger stages which can be succeeded developmentally by specimens such as ours which are of middle to late growth stages.

The largest of the whorls measured by Atabekian (1985, p. 29) is 50 mm in diameter, but in GS. G188 (Figure 4-2) from Hokkaido the diameter of the whorl preceding the last is 62 mm. The last whorl (i.e., body chamber) of this shell is deformed, but it has an eroded remnant of the rostrum and, thus, represents an adult shell.

Occurrence.—As for material.

Discussion.—The relationship between *M. (M.) bergeri* and *M. (M.) miliaris* has been discussed by previous authors. Morphologically and also stratigraphically they are intimate. They cannot be distinguished by the difference in apical angle, since the extent of variation in the angle is great in both species.

The proportion of the height (H) to diameter (D) of a whorl is fairly constant in our specimens, 0.46 to 0.48 (see Table 2). This is the same as that of the holotype, in which $D=37.5$, $H=18.0$, $H/D=0.48$ on the basis of Renz' (1968, pl. 18, fig. 10) illustration. A similar value can be estimated for the whorls of many, if not all, of the illustrations of less deformed specimens of *M. (M.) bergeri* (e.g., Renz, 1968, pl. 18, figs. 3, 4 ;

Table 2. Measurements of *Mariella (Mariella) miliaris* (Pictet and Campiche).

| Whorl (Order)* | 1st | 2nd | 3rd | 4th |
|---|------|------|-------|------|
| Measured specimen : GS. G186 (Figure 4-1) | | | | |
| Diameter (in mm) | 31.0 | 35.2 | 39.2 | 44.0 |
| Height (in mm) | 14.2 | 16.8 | 18.7 | — |
| Height/Diameter | .46 | .48 | .48 | — |
| Tubercles per whorl | 36 | 36 | 36 | 35 |
| Measured specimen : GS. G188 (Figure 4-2) | | | | |
| Diameter (in mm) | 42.0 | 52.6 | ~60.0 | — |
| Height (in mm) | 19.5 | 25.2 | 28.0 | 31.5 |
| Height/Diameter | .46 | .48 | .47 | — |
| Tubercles/half whorl | 17 | 18 | ~17 | — |

* : as for Table 1. ~ : approximate

Atabekian, 1985, pl. 2, figs. 4, 5 ; pl. 3, fig. 9). This is another feature that shows the resemblance between the two species.

A sole distinction between the two species is in the ornamentation, namely finer, denser and more numerous ribs and tubercles in *M. (M.) miliaris* in comparison with *M. (M.) bergeri*. In both species, however, there is a considerable variation even in this. The number of tubercles to a whorl is recorded to extend from 33 to 54 in *M. (M.) miliaris* against 25 to 30 in *M. (M.) bergeri*. Thus, the extent of variation in the number of tubercles appears to be continuous between the two taxa. A statistical examination would give a clear solution of the problem.

Stratigraphically *M. (M.) miliaris* has been recorded from the Upper Albian *dispar* Zone in many cases, but in England it is reported also from the Lower Cenomanian (Wright and Kennedy, 1996, p. 333). Our present material suggests, if not clearly indicates, the occurrence in the lower part of the Cenomanian in Hokkaido.

Mariella (Mariella) cf. carrancoi (Böse, 1923)

Figure 4-3

Compared.—

Turrillites carrancoi Böse, 1923, p. 147, pl. 10, figs. 25-31.

Turrillites multipunctatus Böse, 1923, p. 154, pl. 10, figs. 48-58.

Mariella (Mariella) carrancoi (Böse). Clark, 1965, p. 44, pl. 13, figs. 1-4, 7, 10.

Lectotype.—IGM. 1076-C, figured by Clark, 1965, pl. 13, fig. 3 (designated by Clark, 1965, p. 44).

Material.—GK. H8507 (Figure 3-3) and GK. H8508-H8511 from a transported nodule collected by Nishida and others on 20 August 1988 at loc. R449 of the upper reaches of the Suribachi-zawa (for the location see Matsumoto and Nishida, 1999, fig. 6). The nodule is inferred to have been derived from the Member My3 from its location and lithology, although the sandstones and mudstones in thin-bedded alternation like those of the Member My2 crop out narrowly between R456 and R460.

Description.—The specimens are more or less incomplete ; six whorls are preserved in GK.H8507, three in H8508, two in H8509, slightly over one in H8510 and only one in H8511.

They are small ; the largest one, H8507, is about 30 mm in tower height and 17 mm in diameter of the last whorl. The apical angle is 43° in H8507 and H8508 but maybe somewhat more acute in H8509. The whorl is subquadrate in section with a trapezoidal flank. The ratio of height to diameter in each whorl is very low, about 0.33 to 0.35 in H8507 and H8508, but it varies to some extent with growth and also between individuals (e.g., 0.42 in H8509). Whorls are tightly coiled and their junction is deep.

The main part of the flank is ornamented by two rows of relatively coarse tubercles, with an apparent spiral groove between them. This feature is more pronounced on young whorls where these tubercles show nodular protuberances and are apparently crowded. The tubercles of the third row are disposed along the lower whorl seam. Those of the fourth row are on the lower whorl face and concealed by the succeeding whorl, unless the basal surface is exposed. The number of tubercles per whorl is 24 to 27. Ribs are scarcely discernible on the younger whorls, but on later whorls the tubercles of the first row extend shortly upward in riblike fashion, the tubercles of the second row are somewhat transversely elongated as if connected with the tubercles of the third row, which in turn give rise to radial ribs on the lower face. The tubercles of the fourth row are tiny and each rests on a rib. This feature is observable partly in GK. H8508 and impressed on the upper surface of GK. H8509.

Suture (E/L saddle and L) is partly discernible on the flank of the middle-aged whorl in GK. H8507.

Comparison.—The above-described specimens are rather peculiar to Japan, but they are well comparable with *M. (M.) carrancoi* (Böse), from the "Vraconian" of Zacatecas, Mexico, redefined by Clark (1965, p. 44, pl. 13, figs. 1-4, 7, 10). Although the absence of ribs is taken as a character of this species by Clark and also by Klinger and Kennedy (1978, p. 31), this is applied to the flank ornament of rather earlier growth stages. At least the riblike extension is observable even in the illustration of the lectotype (Clark, 1965, pl. 13, fig. 3) and more elongated ribs are discernible on the whorl of later growth stages in other specimens (e.g., Clark, 1965, pl. 13, figs. 1, 7 and 10). Even in our specimens the mode of lighting, especially its orientation, gives dissimilar appearances to this character. Some of the figures by Böse (1923, pl. 10, figs. 25-31, 48-58) show variation in the ornament between individuals and also with growth. The low ratio between whorl height and diameter is another diagnostic character of this species. The lectotype, measured on the illustration (Clark, 1965, pl. 13, fig. 3), gives 0.31, 0.32, 0.40 and 0.42 in accordance with growth. Our specimens fall in the same ratio range.

To sum up, a set of specimens from loc. R449 can be almost certainly identified with *Mariella (Mariella) carrancoi* (Böse, 1923). However, the five specimens have some deficiencies in preservation. It would be better to call them tentatively *M. (M.) cf. carrancoi*, until material of better preservation is obtained from rocks of a definite stratigraphic level.

Occurrence.—As for material. It should be noted that the present material is inferred to have been derived from the Member My3 of early Cenomanian age, whereas *M. (M.) carrancoi* has been reported to occur in the upper part of the

Albian of Zacatecas, Mexico. The species may range across the Albian–Cenomanian boundary. This should be examined in future.

Mariella (Mariella) gallienii (Boule, Lemoine and Thévenin, 1907)

Figure 5

Turrilites puzosianus d'Orbigny var. *gallienii* Boule, Lemoine and Thévenin, 1907, p. 40, pl. 7, figs. 4, 4a, 4b, 5, 5a.

Turrilites gallienii Boule, Lemoine and Thévenin. Collignon, 1931, p. 89, pl. 9, figs. 15, 16.

Paraturrilites gallienii (Boule, Lemoine and Thévenin). Collignon, 1964, p. 12, pl. 320, figs. 1379, 1380.

Mariella (Mariella) gallienii (Boule, Lemoine and Thévenin) *evoluta* Klinger and Kennedy, 1978, p. 29, pl. 3, figs. C, H, I; pl. 6, figs. B, D, O; pl. 7, figs. A, B; text-figs. 1E; 4E–G.

Mariella (Mariella) gallienii (Boule, Lemoine and Thévenin). Wright and Kennedy, 1996, p. 333, pl. 98, figs. 2, 3, 25, 27; text-fig. 134, D, E, L.

Lectotype.—The original of Boule, Lemoine and Thévenin, 1907, pl. 7, figs. 4, 4a, 4b, from the Cenomanian of Diégo Suarez, northeastern Madagascar (designated by Wright and Kennedy, 1996, p. 333).

Material.—GS. G189 (Figure 5-1), GS. G190 (Figure 5-2, 3), GS. G191 (Figure 5-4), GS. G192 (half ammonoid preservation) and GS. G193 (fragmentary), collected by Y.K. and N. Egashira on 21 June 1996 from a nodule contained in the mudstone of the Member My3 at loc. R906 of the Hotei-

zawa, Soeushinai area (for the location see fig. 7 in Part 1).

Description.—GS. G189 consists of two tightly coiled whorls, although the earliest part is unpreserved. Its whorl is subrounded in cross section, with a broadly convex main part of the flank which passes across the abruptly rounded shoulder to the narrow upper face and likewise downward to the gently convex lower surface. The estimated apical angle is high (60°). The ornament of this specimen consists of numerous, densely disposed, weakly oblique ribs on which small tubercles are set in four rows at subequal intervals. The ribs start at the upper whorl seam and run across the upper shoulder to the main part of the flank and further across the lower shoulder to the basal surface. The ribs are thus continuous, but they slightly weaken at the interspaces of the three tubercles, resulting in two shallow spiral depressions on the flank (Figure 5-1a, b). The tiny fourth tubercles are discernible on the basal surface where ribs run to the umbilical margin with a gentle curvature (Figure 5-1c).

The three specimens, GS. G190–G192, show a tall turreted shape, consisting of several (4 to 6) whorls. They seem to show an apparently low apical angle, but the actual apex is not known, because several whorls of the youngest stage are not well shown. The whorls are rather loosely coiled in the main to later growth stages and the last one (body chamber) is detached in GS. G191 (Figure 5-4), although this feature might be secondary. It should be noted that the whorls in earlier stages seem to be fairly tightly coiled (Figure 5-2, 3, 4). In the young stage of these specimens the whorl shape is fairly similar to that of the above small specimens

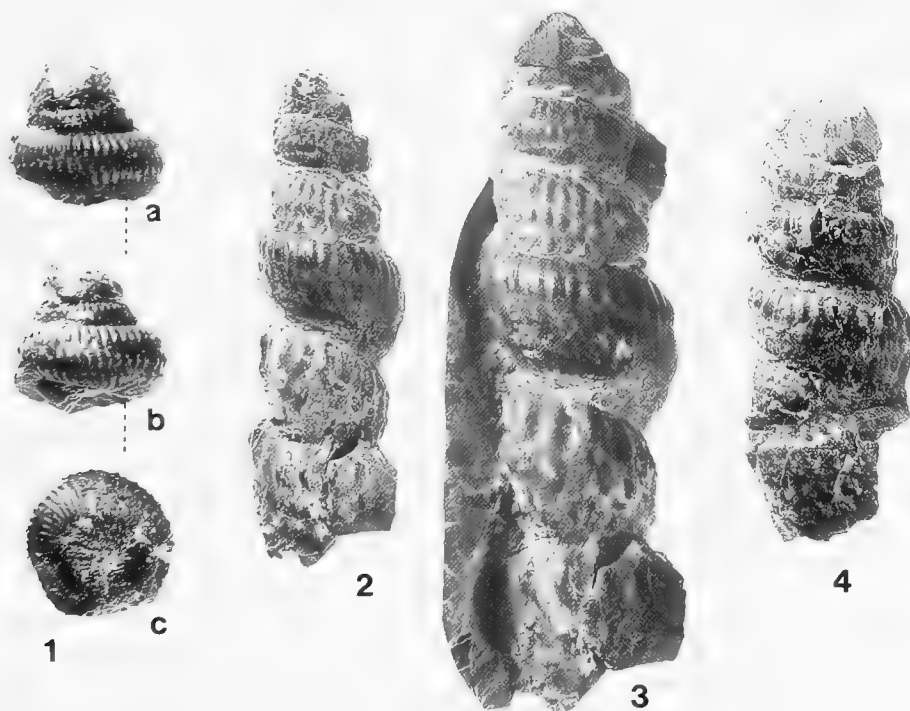


Figure 5. *Mariella (Mariella) gallienii* (Boule, Lemoine and Thévenin). 1. GS. G189, two lateral (a, b) and basal (c) views, $\times 4/3$. 2. GS. G190, lateral view, $\times 1$. 3. GS. G190, lateral view before it is detached from the host rock, $\times 1.4$. 4. GS. G191, lateral view, $\times 4/3$. (Photos by N. Egashira without whitening.)

(GS. G189), but in later stages the whorl becomes increasingly higher, with a weakly convex to nearly flat main flank and a rather oblong section. The ornamentation of these specimens is fundamentally similar to that of the first specimen (GS. G189), but the rib density (or the number of ribs per whorl) varies with growth and between individuals. The variation in the rib density and also in shell shape may be expressed by the columns Ribs and H/D in Table 3. Thus, the ribbing becomes less dense with growth. In GS. G190 the ornament is especially coarse on the loosely coiled last whorl (Figure 5-3).

Septal sutures are observable where the shell layer is taken away, as on the third whorl from the bottom in GS. G190.

Measurements.—See Table 3.

Comparison.—GS. G189 (Figure 5-1) is fairly similar to the lectotype (see above) of this species. Although the ribs are denser in the latter, the difference is by no means great (see Table 3). Our specimen is morphologically intermediate between the lectotype and paralectotype (Boule *et al.*, 1907, pl. 7, figs. 4 and 5) from Madagascar.

The two whorls of the middle growth stage in GS. G190 and GS. G191 resemble those of MNHP R1073 from Madagascar described by Collignon (1931, pl. 9, fig. 16) and reillustrated by Wright and Kennedy (1996, text-fig. 134 L). Another specimen from the lectotype locality in Madagascar, illustrated by Collignon (1964, pl. 320, fig. 1379) and reillustrated by Wright and Kennedy (1996, text-fig. 134E) exemplifies a distinct change of relative whorl diameter at a certain young stage. This may support the presumed shape of the missing or poorly preserved young part of the three specimens (GS. G190-192) mentioned above.

Occurrence.—As for material. Outside Hokkaido, this species has been recorded in the Lower Cenomanian of Madagascar, South Africa and England (see references in the synonymy).

Discussion.—This species was established as a variety of

Ostlingoceras puzosianus. This assignment has been revised by subsequent authors, as indicated in the synonymy list.

Klinger and Kennedy (1978, p. 29, pl. 3, figs. C, H, I; pl. 6, figs. B, D, O; pl. 7, figs. A, B; text-figs. 1E, 4E-G) established a subspecies *M. (M.) gallienii evoluta*, "which is characterized by loose coiling in which successive whorls are only slightly impressed." Although we have not looked at the actual specimen, the holotype of subspecies *evoluta* (*op. cit.*, pl. 6, fig. C) does not seem to be so loosely coiled as the middle-to-late stage of GS. G190 and G191. In our material the mode of coiling (loose or tight coiling) varies with growth and also between individuals. Moreover, the tightly coiled small specimen and larger ones with loosely coiled later whorls are contained in the same nodule. The Hokkaido material shows good conformity with that from Madagascar, which lay close to Zululand in mid-Cretaceous time. Some of the specimens from England (e.g., Wright and Kennedy, 1996, pl. 98, fig. 25) seems to show a rather loose coiling. A specimen from Zululand, donated to GK by Kennedy, is intermediate in the mode of coiling and rib density. For these reasons we are inclined to regard the subspecific separation as unnecessary and unnatural.

Concluding remarks

The genus *Mariella* of the Turrilitidae ranges from the Upper Albian to the Lower Cenomanian and includes a fair number of species. In these two successive papers altogether eight species of the subgenus *Mariella* (*Mariella*) from Hokkaido (northern Japan) have been described.

In Part 1 *M. (M.) dorsetensis* (Spath), *M. (M.) oehlerti* (Pervinquière) and *M. (M.) pacifica* Matsumoto, Inoma and Kawashita have been recorded to occur fairly commonly or very abundantly (the second species) in the Lower Cenomanian of the Soeushinai area (northwestern Hokkaido). *M. (M.) dorsetensis* and *M. (M.) oehlerti* are distributed worldwide in the Lower Cenomanian. They can be regarded as cosmopolitan elements of the fauna and are useful for interregional correlation. *M. (M.) pacifica*, which was established in Part 1, is so far endemic, but its wider distribution would be expected in view of its similarity to *M. (M.) torquatus* Wright and Kennedy and *M. (M.) numida* (Pervinquière) and its having some affinity with late Albian *M. (M.) camachoensis* (Böse).

The five species described in Part 2 are based on a rather small number of specimens, but they are interesting in creating some problems either in taxonomy or in stratigraphic occurrence. *M. (M.) bergeri* was obtained from the upper part of the Member My2 in the Soeushinai area, that is a correlative of the uppermost Albian. One of the specimens shows finely preserved spines. The second species tentatively called *M. (M.) aff. bergeri* is probably new for its particular characters. It came from the lower part of the Member My3, i.e., the basal Cenomanian. The third is identified with *M. (M.) miliaris* redefined by Atabekian (1985). It is based on three specimens which are inferred to have been derived from the Lower Cenomanian. The fourth is referred to *M. (M.) cf. carrancoi* (Böse). *M. (M.) carrancoi* is originally from the Upper Albian of Mexico, but our material

Table 3. Measurements of *Mariella* (*Mariella*) *gallienii* (Boule, Lemoine and Thévenin).

| Specimen Whorl* | Diameter | Height | H./D. | Ribs |
|-----------------|----------|--------|-------|------|
| GS. G189 (1st) | 10.2 | 3.4 | .33 | |
| GS. G189 (2nd) | 14.5 | 6.5 | .45 | 46 |
| GS. G190 (2nd) | 13.5 | 6.8 | .50 | ~36 |
| GS. G190 (4th) | 20.4 | 13.3 | .65 | 42 |
| GS. G191 (1st) | 17.0 | 6.4 | .38 | ~32 |
| GS. G191 (2nd) | 21.0 | 10.0 | .48 | 34 |
| GS. G191 (3rd) | 23.0 | 13.5 | .59 | 37 |
| Lectotype | 16.0 | 7.5 | .47 | 50 |
| GK specimen | 19.0 | 10.5 | .55 | 34 |

* The order in the column "Whorl" as for Table 1. Ribs: number of ribs per whorl; ~approximate number of ribs estimated from the measurable number in case of half whorl preservation. Lectotype is measured on the illustration in Boule *et al.*, 1907, pl. 7, fig. 4a, b. GK specimen means an example from the Lower Cenomanian I at Skoenberg, Zululand, South Africa, kindly donated by W. J. Kennedy.

probably came from the Lower Cenomanian. The fifth is *M. (M.) gallienii* from the Lower Cenomanian. The subspecific separation of *M. (M.) gallienii gallienii* and *M. (M.) gallienii evoluta* may be unnecessary, for the reasons stated.

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Planktonic foraminifera and biochronology of the Cenomanian–Turonian (Cretaceous) sequence in the Oyubari area, Hokkaido, Japan

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Abstract. A Cenomanian and Turonian (Late Cretaceous) sequence along the Shirakin River, Oyubari area, central Hokkaido, Japan contains seven datum planes of planktonic foraminifera that can be used to establish international correlations. These datum planes are marked by the first appearance of *Praeglobotruncana gibba*, *Rotalipora greenhornensis*, *Rotalipora deecke*, *Marginotruncana schneegansi* and *Marginotruncana pseudolinneana*, and the last appearance of *Rotalipora deecke* and *Rotalipora cushmani*. These datum planes can be correlated with international Cretaceous planktonic foraminiferal zones in the interval KS17–KS22. Seventeen planktonic foraminiferal species are described including five new species: *Hedbergella kyphoma*, *Praeglobotruncana compressa*, *Praeglobotruncana inermis*, *Praeglobotruncana shirakinensis*, and *Dicarinella takayanagii*.

Key words: biostratigraphy, Cenomanian, Cretaceous, datum plane, planktonic foraminifera, Turonian, Yezo Group

Introduction

The Cretaceous Yezo Group in Hokkaido, Japan yields abundant ammonites and inoceramids that have been used to create a number of regional biostratigraphic zones. However, most of these molluscan fossils cannot be used for high resolution biochronology and international correlation (e.g. Matsumoto, 1942, 1943; Hirano *et al.*, 1977, 1981; Hirano, 1982). On the other hand, there have been few biostratigraphic studies of calcareous microfossils in the Yezo Group. A planktonic foraminiferal biostratigraphy of the Yezo Group was first established by Takayanagi in 1960. Subsequently, Takayanagi and Iwamoto (1962) and Takayanagi and Okamura (1977) have reported planktonic foraminiferal occurrences from the group. Maiya and Takayanagi (1977) and Maiya (1985) summarized a Japanese planktonic foraminiferal zonation. However, these zonations have not been adequate for detailed interregional correlation of local Japanese Cretaceous sequences. In this decade, Motoyama *et al.* (1991), Hasegawa and Saito (1993), Hasegawa (1997) and Takashima *et al.* (1997) reported Cretaceous planktonic foraminiferal biostratigraphy from the Oyubari area of central Hokkaido and their reported taxa suggest that age-diagnostic species are available for international correlation. Nishida *et al.* (1993) presented additional data on the

biostratigraphic correlation of the Oyubari sequence based on micro- and megafossils. Hasegawa (1995) further clarified the precise stratigraphic position of the last appearances of *Rotalipora greenhornensis* and *Rotalipora cushmani* and of the first appearance of *Marginotruncana schneegansi* near the Cenomanian/Turonian (C/T) boundary. Recently, Hasegawa (1997) used a comprehensive biostratigraphy of planktonic foraminifera to demonstrate interregional synchronicity of carbon isotopic events during Cenomanian–Turonian age. However, with the exception of Kaiho's (1992) work on Campanian species, no descriptive work on planktonic foraminiferal species of the Yezo Group has been presented in recent years.

This study describes seven planktonic foraminiferal datum planes recognized in the Cenomanian–Turonian sequence exposed along the Shirakin River in the Oyubari area and attempts biostratigraphic correlation with the international zonation established by Sliter (1989). Planktonic foraminiferal species, including twelve age-indicative species and five new species, are described.

Materials and methods

Samples used in this study were collected from the Yezo Group mainly along the Shirakin (=Hakkinzawa) River,

Oyubari area, central Hokkaido, Japan (Figures 1, 2). The Yezo Group is interpreted as a forearc basin facies (Okada, 1979, 1983). In the Oyubari area, the Cenomanian–Turonian sequence of the group is represented by the Hikagenosawa and Takinosawa Formations as defined by Motoyama *et al.* (1991). Approximately 300 samples were collected and processed. Near the C/T boundary, sampling was at approximately 2.5 m intervals. Faunal analyses are based on 49 planktonic foraminifera-bearing samples consisting largely of siltstone in the Cenomanian–Turonian section. Samples weighing approximately 240 g were disaggregated using sodium sulfate, naphtha solution (Maiya and Inoue, 1973), and sodium tetraphenylborate plus sodium chloride (Hanken, 1979), washed through a 63 μm screen and dried. All specimens larger than 180 μm were identified. Additionally, larger samples (500–800 g) were analyzed in the boundary sequence from 7 m below to 40 m above the C/T boundary. All specimens described herein are deposited in the Department of Geoenvironmental Science, Faculty of Science, Tohoku University.

Biostratigraphy

The planktonic foraminiferal assemblages are listed in Table 1. A detailed biostratigraphy near the C/T boundary has been established along the Shirakin River, based on continuous occurrences of planktonic foraminifera (Hasegawa, 1995; Hasegawa, 1997). Common occurrence of internationally recognized species, especially those within the genera *Rotalipora* and *Marginotruncana* allow correlation with datum planes as summarized by Caron (1985) and Sliter (1989).

The stratigraphic distribution of planktonic foraminifers in the Oyubari section is shown in Figures 3 and 4. In addition, two late Cenomanian samples collected from the Kashima–migimata River (Figure 2) are included in the data presented in Figure 3. Although the Hikagenosawa Formation (Figure 3) includes a low-diversity assemblage, several species have biostratigraphic utility, including *Rotalipora gandolfii* (Luterbacher and Premoli-Silva) from the lower to middle, and *Praeglobotruncana gibba* Klaus, *Rotalipora greenhornensis* (Morrow) and *Rotalipora deeckeii* (Franke) from the uppermost part of the formation. On the other hand, the lower part of the Takinosawa Formation is characterized by highly diversified assemblages including such international zonal species as *Rotalipora cushmani* (Morrow) and *Helvetoglobotruncana helvetica* (Bolli) as well as the age-indicative species *R. greenhornensis*, *R. deeckeii* and *Marginotruncana schneegansi* (Sigal). In the middle to upper part of the Takinosawa Formation and in the overlying Shirogane Formation, the planktonic foraminiferal diversity declines again, with only two biochronologically important species, *Marginotruncana pseudolinneiana* Pessagno and *Marginotruncana coronata* (Bolli), having correlational significance.

Datum planes

Based on the stratigraphic distribution of the species that belong to the genera *Rotalipora* and *Marginotruncana* and other important age-diagnostic species (e.g., *Helvetoglobotruncana helvetica* and *Praeglobotruncana* spp.), seven bioevent horizons (i.e., FAD, first appearance datum; LAD, last appearance datum) were recognized in the Shirakin River section as reliable datum planes. These are discus-



Figure 1. Index map showing the locality of the Oyubari area.

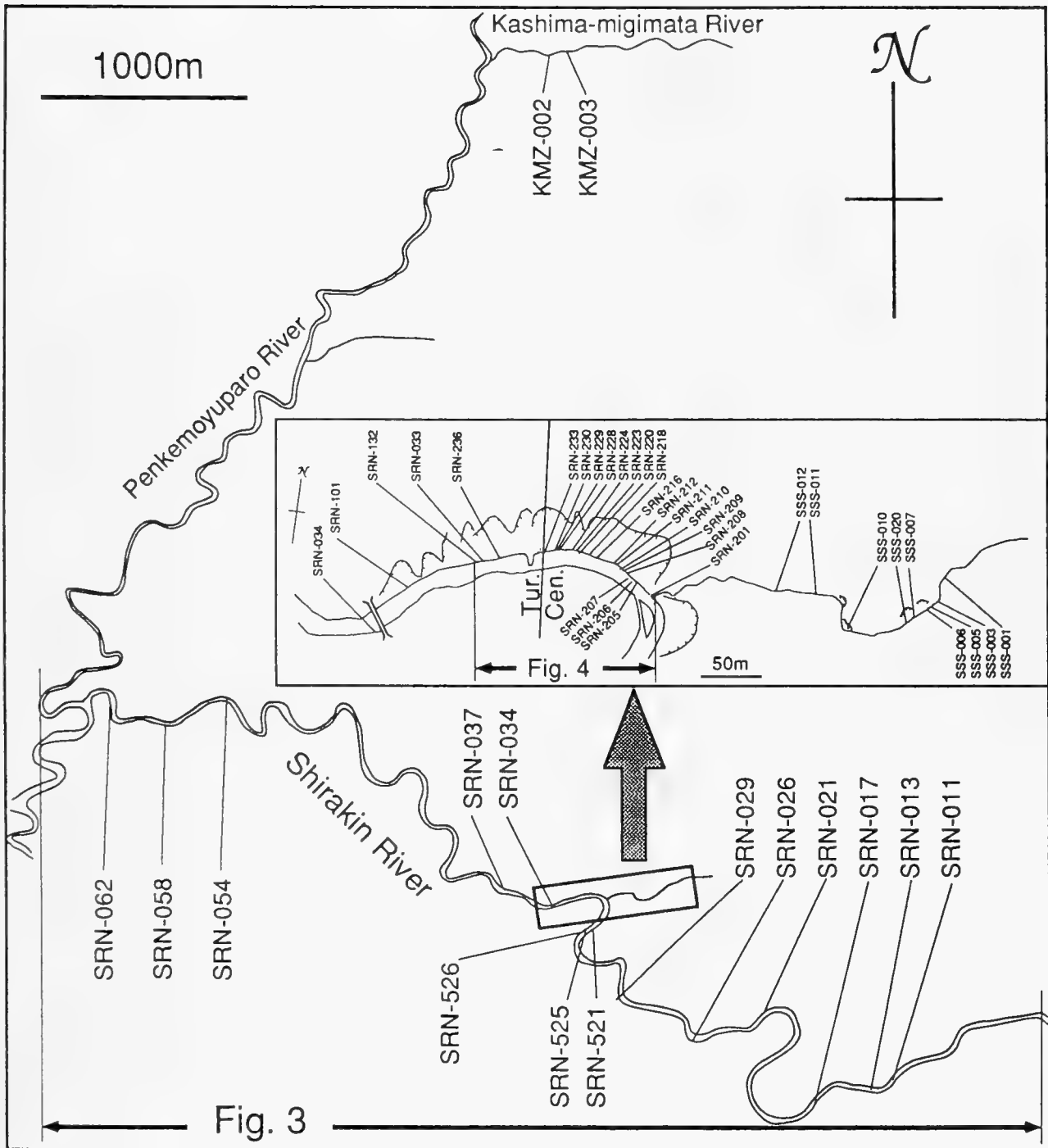


Figure 2. Map showing sampling localities in the Oyubari area.

sed separately below.

A: FAD of *Praeglobotruncana gibba*

This datum is early Cenomanian. FAD of *P. gibba* in the middle part of the Hikagenosawa Formation is observed about 180 m below the FAD of *R. greenhornensis*. Accord-

ing to Caron (1985), the FAD of *P. gibba* is located just below the FAD of *R. greenhornensis*, which is consistent with its first occurrence in the Oyubari section. *Rotalipora brotzeni* first occurred above this datum, but its occurrence is too rare to establish a reliable datum level. The planktonic foraminiferal assemblage below this datum is mainly composed

Table 1. Stratigraphic occurrences of planktonic foraminifera in the Oyubari area. Symbols denote the number 2" or "1/4" written under the total number mean that 1/2 or 1/4 fraction of residues of 240 g rock samples were rences shown with parentheses indicate the inclusion of specimens of which specific name can only be given with

| Species | | sample No. | SRN 011 | SRN 013 | SRN 017 | SRN 021 | SRN 022 | SRN 025 | KMZ 003 | SRN 026 | SSS 001 | SSS 003 | KMZ 002 | SSS 005 | SSS 006 | SSS 007 | SSS 020 | SSS 010 | SSS 011 | SSS 012 | SRN 029 | SRN 201 | SRN 205 | SRN 206 |
|-----------------------------|-------------------------------|------------|------------|------------|------------|------------|------------|------------|------------|------------|------------|------------|------------|------------|------------|------------|------------|------------|------------|------------|------------|------------|------------|------------|
| <i>Globigerinelloides</i> | <i>ultramicra</i> | | | | | | | | R | | | F | R | | | | | | | | | | | |
| G. | <i>cf. bentonensis</i> | | | | | | | | | | | | | | | | | | | | | | | |
| G. | <i>cf. eaglefordensis</i> | | | | | | | | | | | | | | | | R | | | | | | | |
| G. | spp. | | | | | | | | | | | | | | | | | | | | | | | |
| <i>Hedbergella</i> | <i>delrioensis</i> | | C | R | F | | | | | R | A | VA | F | C | VA | R | R | R | F | (A) | | | | |
| H. | <i>planispira</i> | | F | R | R | | | | F | | | VA | | R | | | | | R | C | | | | |
| H. | <i>kyphorma</i> sp. nov. | | | | | | | | F | | | | | | | | | | | | | | | |
| H. | spp. | | | | | | | | | | R | | | | | | | | | | | | | |
| <i>Rotalipora</i> | <i>cf. appenninica</i> | | | | | | | | | | R | | | | | | | | | | | | | |
| R. | <i>gandolfii</i> | | | | R | | | | R | | | | | | | | R | | | | | | | |
| R. | <i>brotzeni</i> | | | | R | | | | R | | | | R | F | F | | | | | | | | | |
| R. | <i>greenhornensis</i> | | | | F | | | R | C | | | R | | F | | | | | | | | | | R |
| R. | <i>deeckeii</i> | | | | | | | | R | | | | F | | | | | | | | | | | |
| R. | <i>cushmani</i> | | | | | | | | | | | | | | F | R | | | | | | R | | |
| R. | spp. | | | | R | | | | | | | | R | | | | | | | | | | | |
| <i>Praeglobotruncana</i> | <i>delrioensis</i> | R | | A | VA | R | | | | A | R | A | | C | C | F | | C | A | C | | R | R | R |
| P. | <i>stephani</i> | | | C | VA | R | R | | | A | VA | C | F | VA | F | | R | A | VA | C | A | R | A | F |
| P. | <i>gibba</i> | | | F | A | | | | | A | A | C | | A | F | F | F | R | A | C | F | R | A | C |
| P. | <i>anumalensis</i> | | | | R | | | | | | VA | VA | R | VA | VA | | | | VA | A | F | | A | C |
| P. | <i>shirakinensis</i> sp. nov. | | | | A | | | | | | C | | | | | | | | | | | | C | C |
| P. | <i>inermis</i> sp. nov. | | | | | | | | | R | A | C | | F | F | R | | | C | R | | | A | |
| P. | <i>compressa</i> sp. nov. | | | | | | | | | | | | | | | R | | F | F | | R | R | C | |
| P. | spp. | | | | | | | | | | A | C | | C | R | | | | A | F | | R | A | |
| <i>Whiteinella</i> | <i>cf. archaeocretacea</i> | | | | | | | | | | A | R | | | F | R | | R | | | | | R | |
| W. | <i>aprica</i> | | | | | R | | R | | | | | | | | | | | C | (F) | | | | |
| W. | <i>baltica</i> | | | | | | | | | | | A | | F | A | | | | C | | | | | |
| W. | <i>brittonensis</i> | | | | | | | | | | F | A | | | | | | | R | (R) | | | | |
| W. | <i>inornata</i> | | | | | | | | | | | | | | | | | | | | | | | |
| W. | spp. | | | | | | | | | | C | | | | F | | R | C | A | | | | C | |
| <i>Dicarinella</i> | <i>imbricata</i> | | | | | | | | | R | F | | | | | R | | | | R | | | F | |
| D. | <i>canaliculata</i> | | | | | | | | | | A | | | | | | | | | | | | | |
| D. | <i>takayanagi</i> sp. nov. | | | | | | | | | | A | | | (R) | | | | | | | | | | |
| D. | <i>hagni</i> | | | | | | | | | | | | | | | | | | | (R) | | | | |
| D. | <i>roddai</i> | | | | | | | | | | | | | | | | | | | | | | | |
| D. | <i>japonica</i> | | | | | | | | | | | | | | | | | | | | | | | |
| D. | spp. | | | | | | | | | | R | | | | | R | | | | | | | | |
| <i>Helvetoglobotruncana</i> | <i>helvetica</i> | | | | | | | | | | | | | | | | | | | | | | | |
| <i>Marginotruncana</i> | <i>marginata</i> | | | | | | | | | | | | | | | | | | | | | | | |
| M. | <i>schneegansi</i> | | | | | | | | | | | | | | | | | | | | | | | |
| M. | <i>pseudolinneiana</i> | | | | | | | | | | | | | | | | | | | | | | | |
| M. | <i>cf. coronata</i> | | | | | | | | | | | | | | | | | | | | | | | |
| Indeterminable specimens | | | 1 | 4 | 1 | | 1 | 0 | 0 | 9 | 34 | 11 | 1 | 30 | 24 | 10 | 1 | 3 | 23 | 11 | 2 | 0 | 17 | 0 |
| Total number | | | 2 | 14 | 28 | 335 | 7 | 2 | 20 | 56 | 132 | 103 | 22 | 164 | 154 | 25 | 9 | 29 | 100 | 109 | 15 | 9 | 110 | 19 |
| | | | | | | | | | | (1/2) | (1/2) | | | (1/2) | | | | | | | | | | |

of long ranging species such as *Hedbergella delrioensis* (Carsey), *Hedbergella planispira* (Tappan), *Globigerinelloides ultramicra* (Subbotina), *Praeglobotruncana delrioensis* (Plummer) and *Praeglobotruncana stephani* (Gandolfi).

B: FAD of *Rotalipora greenhornensis*

This datum is early-middle Cenomanian. The FAD of *Rotalipora greenhornensis* occurs in the upper part of the Hikagenosawa Formation. According to Caron (1985) and Sliter (1989), *R. greenhornensis* and *R. cushmani* have the same FAD. However, *Rotalipora cushmani* first occurs above the FAD of *R. greenhornensis* in the Oyubari section. The first occurrence of *R. cushmani* in the Oyubari section is observed above the LAD of *Rotalipora deeckeii* and even above the first-occurrence horizon of the genus *Dicarinella*. This delayed first occurrence of *R. cushmani* is interpreted as a migration event of this species in this area. The strati-

graphic relationship of the FAD of *R. greenhornensis* with other bioevents is concordant with that shown by Caron (1985) and Sliter (1989). The planktonic foraminiferal assemblage between the FAD of *P. gibba* and the FAD of *R. greenhornensis* is similar to that occurring below the FAD of *P. gibba*.

C: FAD of *Rotalipora deeckeii*

This datum is late Cenomanian. *Rotalipora deeckeii* is a short-ranging age-diagnostic species of late Cenomanian age. According to Sliter (1989) and Robaszynski and Caron (1979), the total range of *R. deeckeii* characterizes the upper part of the *Rotalipora cushmani* Zone (the range of *Rotalipora deeckeii* is not shown in the range distribution chart of Caron, 1985). Stratigraphically, the FAD of *R. deeckeii* lies near the top of the Hikagenosawa Formation. The occurrences of *Whiteinella* spp. and *Dicarinella* spp. within the total range of

of specimens included in each 240 g rock sample. VA: >21 specimens, A: 10~20, C: 6~9, F: 3~5, R: 1 or 2. "1"/examined. The abundance of those samples are indicated by converted number into 240 g equivalent. The occur-"cf.". The specimens of which species name bear "aff." are indicated by italic.

[illegible]

R. deecke indicate that both the FAD and LAD of *R. deecke* are reliable datum planes in the Oyubari section. Between FADs of *R. greenhornensis* and *R. deecke*, the species *Praeglobotruncana anumalensis* (Sigal) and *Praeglobotruncana shirakinensis* n. sp. appear. However, the constituent species of the assemblage are similar to those occurring below the FAD of *R. greenhornensis*. The last occurrence of *Rotalipora gandolfii* Luterbacher and Premoli-Silva is observed at the same level as the FAD of *R. deecke*, which shows considerable inconsistency with their stratigraphic relationship as summarized by Sliter (1989) and Caron (1985). Apparently *R. gandolfii* survived later in the northwestern Pacific.

D: LAD of *Rotalipora deecke*

This datum is late Cenomanian. The LAD of *Rotalipora deeckeii* is recognized near the bottom of the Takinosawa

Formation. A drastic faunal turnover was observed within the total range of *R. deeckeae*. This faunal modification is characterized by the entry of *Dicarinella* spp., *Whiteinella* spp. and *Præglobotruncana inermis* n. sp.

E: LAD of *Rotalipora cushmani*

This datum is latest Cenomanian. The last occurrence of *Rotalipora cushmani* is observed at the same horizon as that of *Rotalipora greenhornensis*. Caron (1985) and Sliter (1989) reported the LAD of *R. greenhornensis* just below the LAD of *R. cushmani*. However, recent precise biostratigraphical studies of planktonic foraminifera indicate that these LADs are almost synchronous. Leckie (1985) described a Cenomanian/Turonian planktonic foraminiferal biostratigraphy in Pueblo, Colorado, for one of the best studied Cenomanian/Turonian boundary sections, in which *R. greenhornensis* and *R. cushmani* show synchronous last

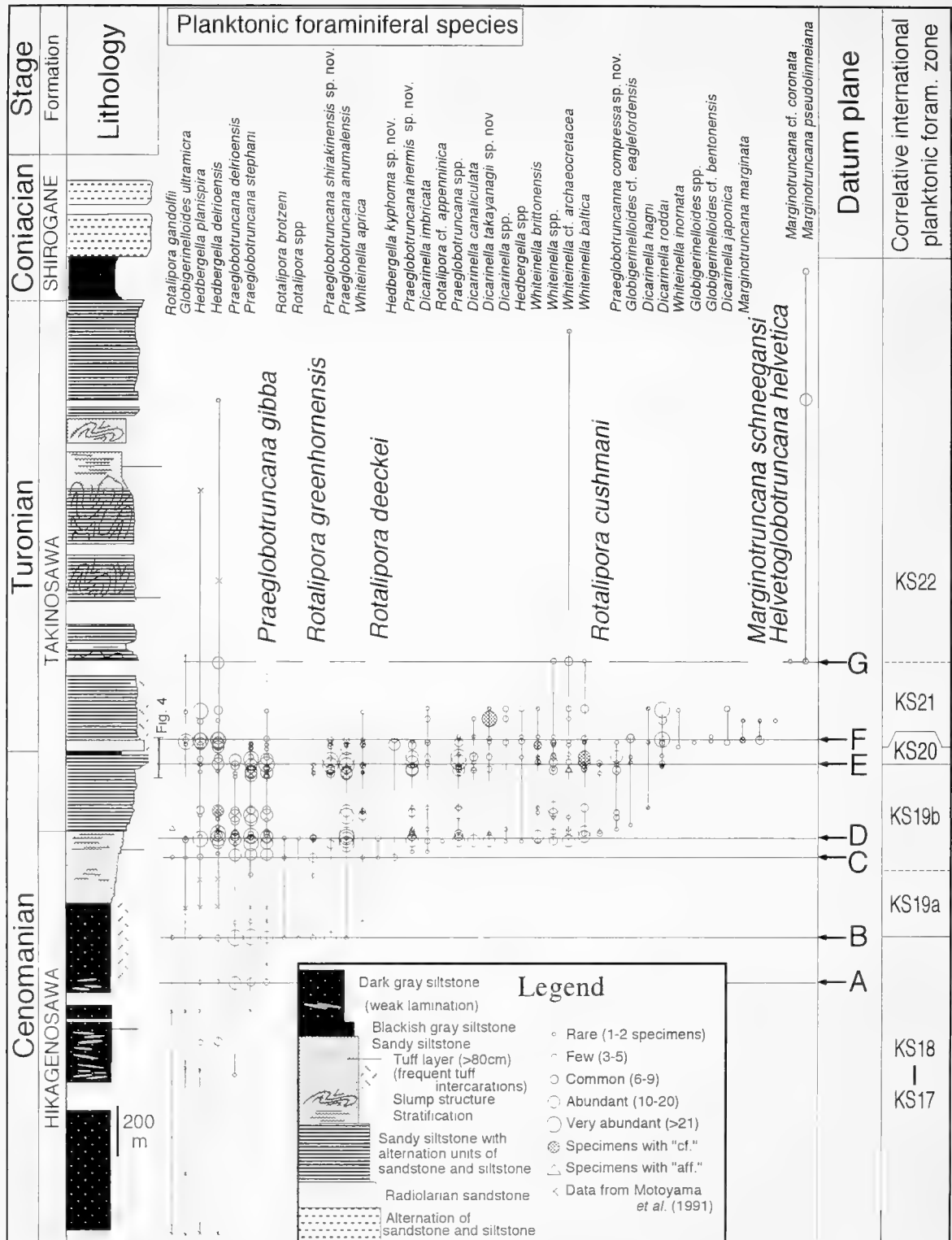
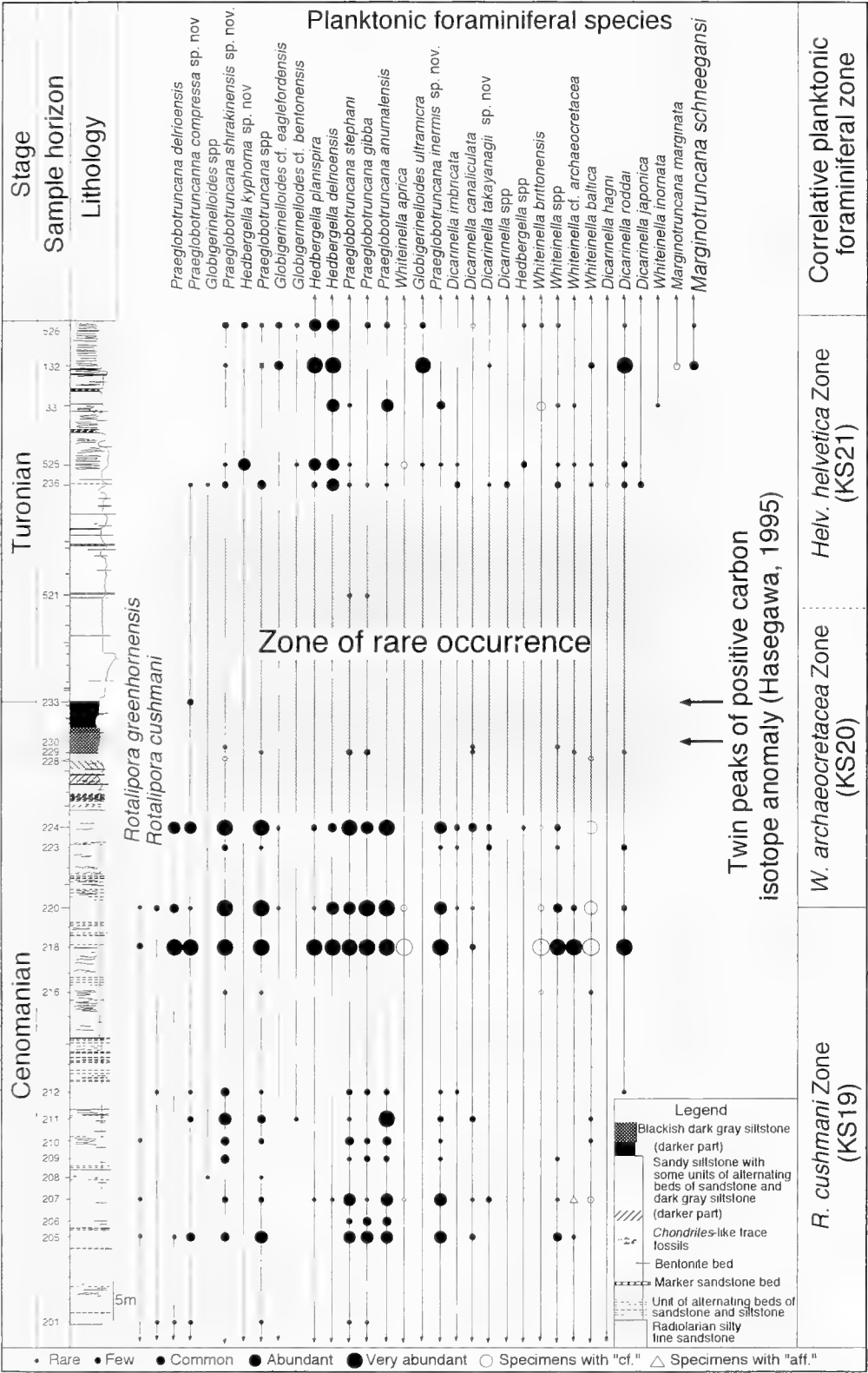


Figure 3. Stratigraphic distribution of planktonic foraminiferal species along the Shirakin River and the tributary of Penkemoyuparo River in the Oyubari area (reproduced from Hasegawa, 1997, with permission from Elsevier Science). Seven reliable datum planes are recognized in the section (see text for notation of datum planes). Symbols denote the number of specimens included in each 240 g rock sample.



occurrences. Jarvis *et al.* (1988) and Hart and Leary (1989) also noted nearly synchronous last occurrences of these two species in Southeast England. Therefore, the LAD of *R. cushmani* observed in Hokkaido is regarded as a reliable datum plane for interregional correlation. The planktonic foraminiferal assemblage between the LAD of *R. deecke* and LAD of *R. cushmani* shows the highest diversity in the Oyubari area. The most abundant species of the assemblage are *Praeglobotruncana* spp. with common *Whiteinella* spp. and less *Rotalipora* spp. and *Dicarinella* spp.

In the northern Oyubari area, Takashima *et al.* (1997) attempted to recognize KS zones (Sliter, 1989). Rare occurrences of *Rotalipora* species did not allow them to correlate their upper Cenomanian sequences to KS zones directly with zone-indicative species. Such rare occurrences of *Rotalipora* may partly depend on the marine paleoenvironment of the northern Oyubari area being a shallower one than in the southern area, where the samples of this study were collected.

F: FAD of *Marginotruncana schneegansi*

This datum is early Turonian. The FAD of *Marginotruncana schneegansi* occurs just above the "Radiolarian sandstone" (Hasegawa and Saito, 1993; Hasegawa, 1995) developed in the lower-middle part of the Takinosawa Formation. *Helvetoglobotruncana helvetica*, which is a commonly used datum species for the recognition of early Turonian age occurred above the FAD of *M. schneegansi*. According to Caron (1985) and Sliter (1989), the concurrent range of these two species is quite restricted. Therefore, the FAD of *M. schneegansi* is interpreted to be a reliable datum plane in Hokkaido. The planktonic foraminiferal assemblage between the LAD of *R. cushmani* and the FAD of *M. schneegansi* is also a high-diversity assemblage except in the middle part of the interval (Figure 4). Between SRN-224 and SRN-236, planktonic foraminifers are rare and the diversity is low despite a high density of large samples (500–800 g). This low-diversity event has also been recognized in other areas of the world (e.g. Hart and Leary, 1989). An oceanic event termed "Oceanic Anoxic Event (OAE)" (Schlanger and Jenkyns, 1970) or "Cenomanian Turonian Boundary Event (CTBE)" (Thurrow and Kuhnt, 1986) may be responsible for this worldwide synchronous phenomenon.

G: FAD of *Marginotruncana pseudolinneiana*

This datum is middle Turonian. The FAD of *Marginotruncana pseudolinneiana* is located in the middle of the Takinosawa Formation and this species is a common one in the

middle Turonian and Coniacian interval. The stratigraphic distributions of other international species across this datum in the Oyubari section are consistent with occurrences known from other parts of the world (e.g. Robaszynski and Caron, 1979; Caron, 1985; Sliter, 1989). Therefore, the FAD of *M. pseudolinneiana* is considered to be a reliable datum plane. The stratigraphic interval between the FAD of *M. schneegansi* and the FAD of *M. pseudolinneiana* yields a moderately diversified assemblage. However, the upper part of this interval and sequence above the FAD of *M. pseudolinneiana* yield less abundant and lowly diverse assemblages.

Recognition of zonal boundary

Stratigraphic units equivalent to the international planktonic foraminiferal zones are recognized in the Oyubari section (Figures 3 and 4) by correlating these datum planes with those shown by Sliter (1989) and Caron (1985). The upper limit of each zone is drawn as follows:

KS18: at the FAD of *R. greenhornensis*;

KS19a: estimated to lie just below the FAD of *R. deecke* and above the FAD of *R. greenhornensis*;

KS19b: at the LAD of *R. cushmani*;

KS20: estimated to lie just below the FAD of *Pseudaspidoceras flexuosum* (an ammonoid) below the FAD of *M. schneegansi* (see Hasegawa, 1995 for further discussion). At the north of the studied area, Takashima *et al.* (1997) recognized the zonal marker species, *Helvetoglobotruncana helvetica*;

KS21: estimated to occur near the FAD of *M. pseudolinneiana*.

Systematic paleontology

Superfamily Rotaliporacea Sigal, 1958

Family Hedbergellidae Loeblich and Tappan, 1961

Subfamily Hedbergellinae Loeblich and Tappan, 1961

Genus *Hedbergella* Bronnimann and Brown, 1958

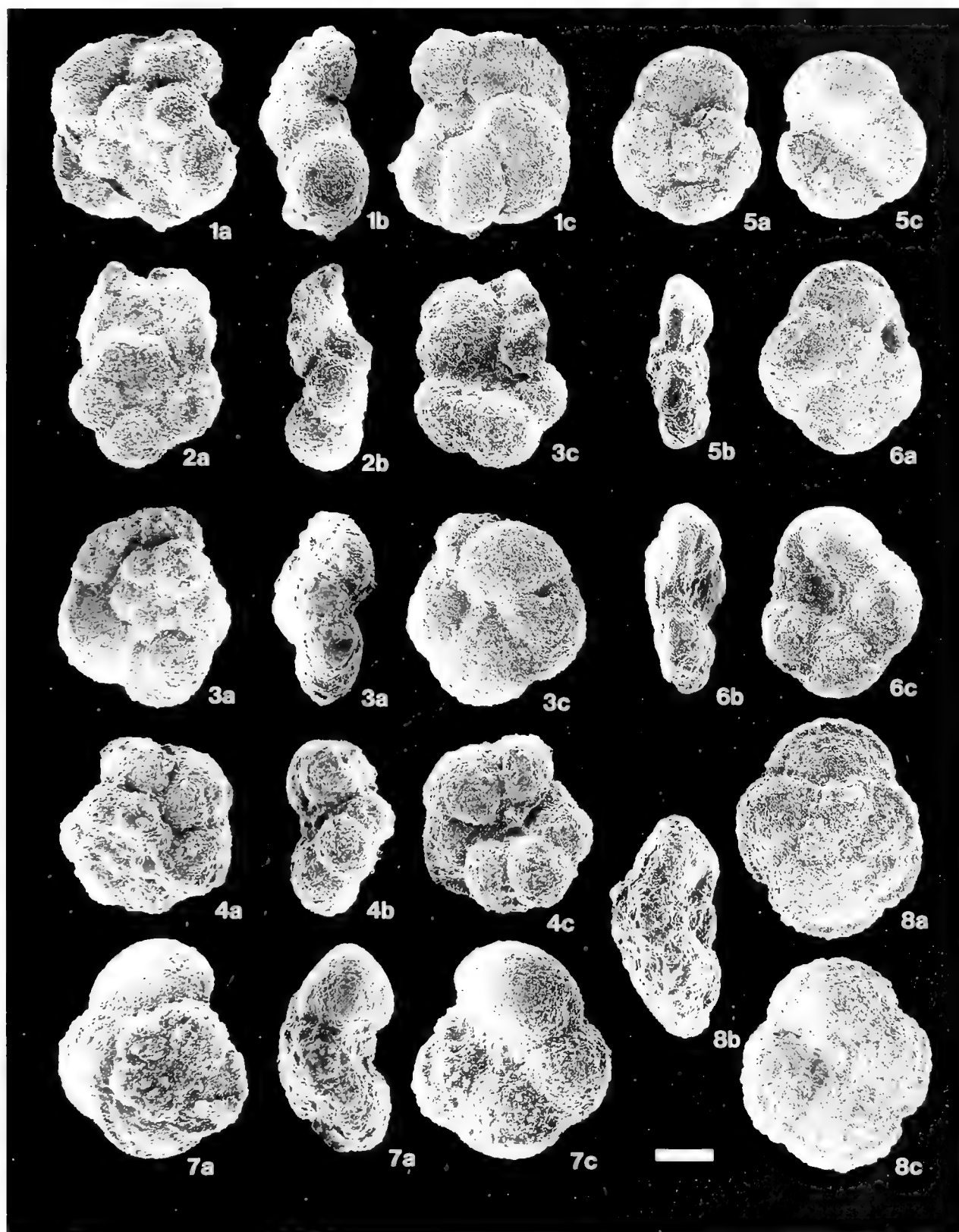
Hedbergella kyphoma sp. nov.

Figures 5–1–4

Diagnosis.—A low trochospiral species of *Hedbergella* with last four chambers umbilically shifted, compressed, and spirally elongate. Umbilicus narrow, sutures of last four chambers slightly curved.

Description.—Test of medium size, initially very low tro-

Figure 5. 1–4. *Hedbergella kyphoma* sp. nov. 1. Holotype, IGPS No. 102504, sample loc. no. SRN-525A, lower part of the Takinosawa Formation, lower Turonian. 2. Paratype, IGPS No. 102505, sample loc. no. SRN-525A, lower part of the Takinosawa Formation, lower Turonian. 3. Paratype, IGPS No. 102506, sample loc. no. SRN-525A, lower part of the Takinosawa Formation, lower Turonian. 4. Paratype, IGPS No. 102507, sample loc. no. SRN-525A, lower part of the Takinosawa Formation, lower Turonian. 5, 6. *Praeglobotruncana compressa* sp. nov. 5. Holotype, IGPS No. 102707, sample loc. no. SRN-207, lower part of the Takinosawa Formation, upper Cenomanian. 6. Paratype, IGPS No. 102708, sample loc. no. SRN-207, lower part of the Takinosawa Formation, upper Cenomanian. 7. Intermediate form between *Praeglobotruncana inermis* sp. nov. and *Praeglobotruncana shirakinensis* sp. nov., IGPS No. 102508, sample loc. no. SRN-210, lower part of the Takinosawa Formation, upper Cenomanian. 8. *Praeglobotruncana shirakinensis* sp. nov., holotype, IGPS No. 102523, sample loc. no. SRN-210, lower part of the Takinosawa Formation, upper Cenomanian. Scale bar=100 μ m



chospiral, later becoming medium trochospiral, equatorial periphery lobulate; chambers initially globular, later slightly compressed and spirally elongated, 11 to 14 in all arranged into 2.5 to 3 whorls, enlarging gradually in size as added except for last 3 or 4 which enlarge irregularly, 6 or 7 in last whorl, last 3 or 4 characteristically elongated, compressed and shifted toward umbilicus, last chamber variable in size and shape; sutures initially radial and depressed on dorsal side except for last 3 or 4 chambers in which they are curved, slightly curved and depressed on ventral side; coiling axis initially stable, later rapidly tilted for last 3 or 4 chambers, as a result, initial umbilicus occasionally being covered by last 3 or 4 chambers; umbilicus shallow, very narrow, less than 1/5 of maximum diameter of test; primary aperture bordered by a narrow lip, interiomarginal, umbilical-extraumbilical, extending to periphery; wall calcareous, surface poorly ornamented.

Remarks.—This species resembles *Hedbergella planispira* (Tappan) in its initially very low trochospiral shape and the number of chambers in the last whorl, but differs from the latter species in having a narrower umbilicus and umbilically shifted and compressed last 3 or 4 chambers.

Etymology.—From *kyphoma*, a Greek noun referring to the humpbacked nature of the pattern of chamber growth in this species.

Material.—Holotype IGPS No. 102504, paratypes IGPS No. 102505 102507.

Dimensions.—Maximum diameter of holotype 0.36 mm, maximum thickness 0.20 mm.

Type locality and horizon.—The holotype and paratypes are all from sample SRN 525A (43°2.50'N, 142°9.72'E), lower part of the Takinosawa Formation, lower Turonian.

Subfamily Rotundininae Bellier and Salaj, 1977

Genus *Praeglobotruncana* Bermudez, 1952

***Praeglobotruncana compressa* sp. nov.**

Figures 5-5, 6

Diagnosis.—A low trochospiral species of *Praeglobotruncana* with compressed and wedge shaped chambers in last whorl.

Description.—Test of medium to small size, very low trochospiral, equatorial periphery slightly lobulate; chambers wedge-shaped on dorsal side, triangular and slightly inflated on ventral side, about 10 chambers in all, enlarging rapidly in size as added, about 4.5 chambers in last whorl, with a peripheral band formed of aligned pustules; final chamber occasionally obliquely shifted toward umbilical direction; chambers in last whorl diagnostically elongated toward spiral direction; sutures on dorsal side gently curved, depressed, ventrally radial or slightly curved and depressed; umbilicus shallow, medium in size, about 1/3-1/4 of maximum diameter of test, umbilical flaps extending into an umbilicus from each chamber; primary aperture bordered by a narrow lip, interiomarginal, umbilical-extraumbilical; wall calcareous, earlier chambers pustulated.

Remarks.—This species is distinguished from *Praeg-*

lobotruncana compressiformis (originally described as *Praeglobotruncana hessi compressiformis* by Pessagno, 1962) and other species of *Praeglobotruncana* in possessing wedge-shaped chambers having depressed sutures in the last whorl on the dorsal side, spirally elongated chambers in the last whorl, and in its generally compressed shape.

Etymology.—From Latin, *compressa* referring to the compressed feature of chambers compared with other species of *Praeglobotruncana*.

Material.—Holotype IGPS No. 102707, paratype IGPS No. 102708.

Dimensions.—Maximum diameter of holotype 0.30 mm, maximum thickness 0.10 mm.

Type locality and horizon.—The holotype and paratype specimens are both from sample SRN-207 (43°2.60'N, 142°9.78'E), lower part of the Takinosawa Formation, upper Cenomanian.

***Praeglobotruncana gibba* Klaus, 1960**

Figure 6-5

Praeglobotruncana stephani (Gandolfi) var. *gibba* Klaus, 1960, p. 304-305, holotype designated in Reichel, 1950, pl. 16, fig. 6, pl. 17, fig. 6.

Praeglobotruncana stephani (Gandolfi). Loeblich and Tappan, 1961, p. 280-284, pl. 6, figs. 4a, b, 5a-c, 6, 7a-c.

Praeglobotruncana gibba Klaus. Robaszynski and Caron, 1979, p. 33-38, pl. 44, figs. 1a-c, 2a-c, pl. 45, figs. 1a-c, 2a-c; Caron, 1985, p. 65, pl. 30-5a-c, 6a-c.

Remarks.—This species is easily distinguished from *Praeglobotruncana stephani* by its high trochospire and from *Praeglobotruncana inermis* n. sp. by its distinct raised suture with a beaded keel on the dorsal side. This species is abundant in the upper part of the *R. cushmani* Zone.

Material.—Hypotype IGPS No. 102503.

Locality and horizon.—The figured specimen is from sample SSS-020, lowermost part of the Takinosawa Formation, upper Cenomanian.

***Praeglobotruncana inermis* sp. nov.**

Figures 6-1-4

Diagnosis.—A high trochospiral species of *Praeglobotruncana* with slight peripheral pustule lines, distinct lip near umbilicus and 4 smooth-walled chambers in last whorl.

Description.—Test of medium to large size, medium to high trochospiral, equatorial periphery lobulate; chambers petaloidal in shape on dorsal side, trapezoidal to subglobular, inflated on dorsal side, about 12 in all arranged into 2 to 2.5 whorls, enlarging gradually in size as added, characteristically 4 chambers in final whorl, with a weak peripheral band formed of an aligned concentration of pustules which tends to be shifted toward spiral side; final chamber shifted toward umbilical direction; sutures on dorsal side radial and depressed except for that of first chamber in last whorl which occasionally is raised, ventrally radial and depressed; umbilicus shallow, medium to narrow in size, less than 1/4 of maximum diameter of test; primary aperture bordered by a

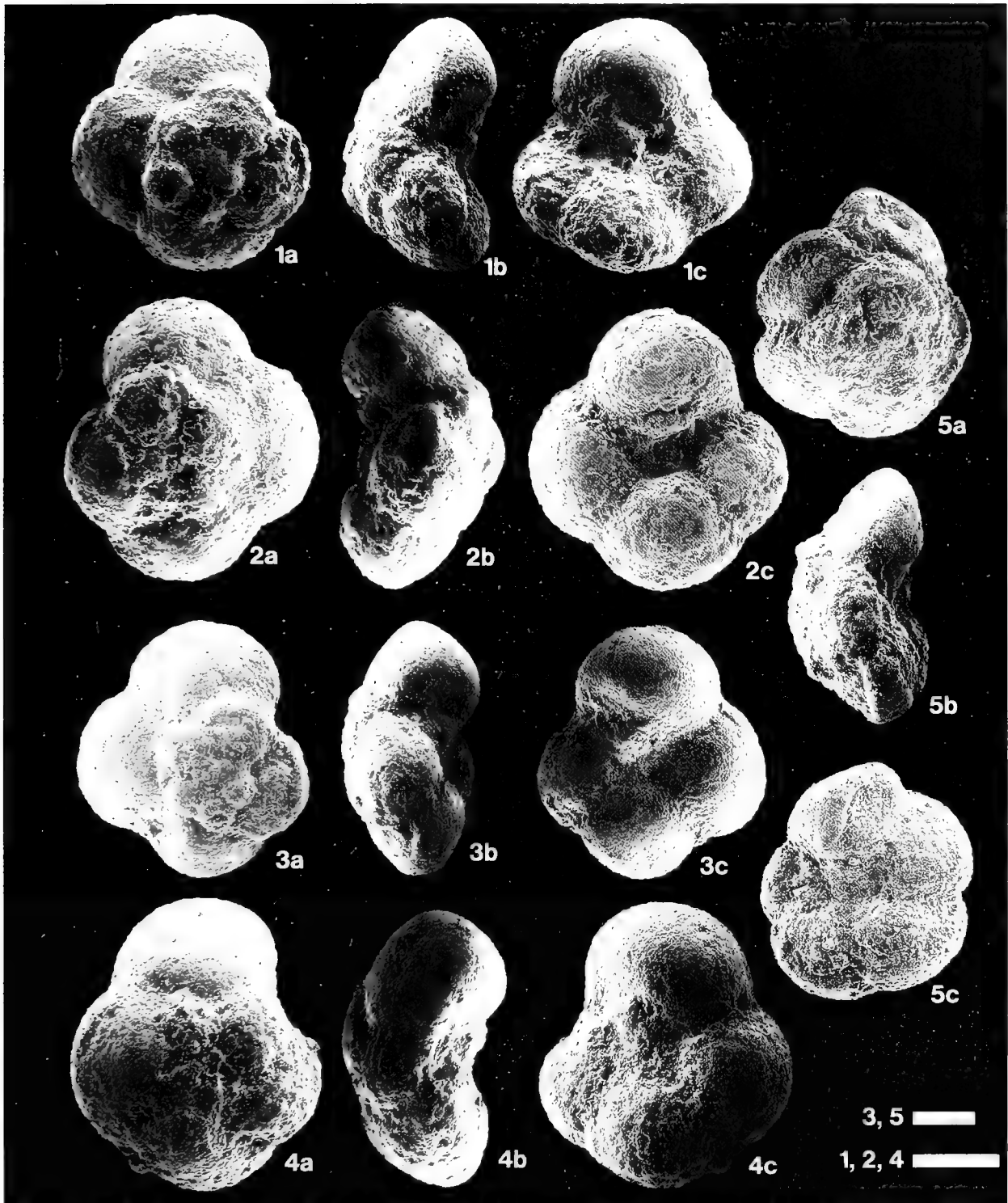


Figure 6. 1–4. *Praglobotruncana inermis* sp. nov. 1. Paratype, IGPS No. 102703, sample loc. no. SRN 220, lower part of the Takinosawa Formation, uppermost Cenomanian. 2. Holotype, IGPS No. 102704, sample loc. no. SRN 220, lower part of the Takinosawa Formation, uppermost Cenomanian. 3. Paratype, IGPS No. 102705, sample loc. no. SRN 220, lower part of the Takinosawa Formation, uppermost Cenomanian. 4. Paratype, IGPS No. 102706, sample loc. no. SRN 220, lower part of the Takinosawa Formation, uppermost Cenomanian. 5. *Praglobotruncana gibba* Klaus, IGPS No. 102503, sample loc. no. SSS 020, lower part of the Takinosawa Formation, upper Cenomanian. Scale bars = 100 μ m.

distinct lip that expands markedly near umbilicus, interiomarginal, umbilical-extraumbilical; wall calcareous, surface smooth, earlier chambers weakly pustulated.

Remarks.—This species closely resembles *Praeglobotruncana anumalensis* (Sigal), but differs in lacking the conspicuous pustules on earlier chambers, in having diagnostically 4 chambers in the last whorl, more lobulated periphery and more inflated chambers.

Etymology.—From Latin, *inermis* referring to the smooth-walled chambers of this species compared with other species of *Praeglobotruncana*.

Material.—Holotype IGPS No. 102704; paratypes IGPS No. 102703, 102705, 102706.

Dimensions.—Maximum diameter of holotype 0.34 mm, maximum thickness 0.21 mm.

Type locality and horizon.—The holotype and paratypes are all from sample SRN-220 (43°2.60'N, 142°9.72'E), lower part of the Takinosawa Formation, uppermost Cenomanian.

***Praeglobotruncana shirakinensis* sp. nov.**

Figure 5-8

Praeglobotruncana sp. Leckie, 1985, p. 139-149, pl. 3, figs 9-15.

Diagnosis.—A medium trochospiral species of *Praeglobotruncana* with about 5 moderately compressed and slightly lobulated chambers of last whorl.

Description.—Test of medium size, medium trochospiral, equatorial periphery slightly lobulate; chambers initially inflated and globigerine-like, later ones becoming petaloidal on dorsal side, trapezoidal in shape on ventral side, about 10 to 12 chambers in all arranged into about 2.5 whorls, enlarging gradually in size as added, about 5 slightly compressed chambers in final whorl, with a peripheral band formed of an aligned concentration of pustules paralleling periphery; sutures on dorsal side curved, raised and beaded, ventrally radial or slightly curved, depressed; umbilicus shallow and narrow, its width about 1/4 of maximum diameter of test; primary aperture bordered by a wide distinct lip, interiomarginal, umbilical-extraumbilical, extending nearly halfway to periphery; wall calcareous, with marked accumulation of pustules on early chambers.

Remarks.—This species resembles *Praeglobotruncana stephani*, but differs in the following characters: spirally slightly elongated and ventrally more inflated chambers of the last whorl; fewer chambers (normally 4 to 5) having almost similar size in the last whorl; less lobulated periphery; and thinner spiral sutures. An intermediate form between *P. inermis* and *P. shirakinensis* is also figured (Figure 5.7).

Etymology.—With reference to the type locality (the Shirakin River) where the holotype specimen occurred.

Material.—Holotype IGPS No. 102523.

Dimensions.—Maximum diameter of holotype 0.38 mm, maximum thickness 0.20 mm.

Type locality and horizon.—The holotype specimen is from sample SRN-210 (43°2.60'N, 142°9.77'E), lower part of the Takinosawa Formation, upper Cenomanian.

Subfamily Helvetoglobotruncaninae Lamolda, 1976

Genus *Helvetoglobotruncana* Reiss, 1957

***Helvetoglobotruncana helvetica* (Bolli, 1945)**

Figure 9-1

Globotruncana helvetica Bolli, 1945, p. 226, pl. 9, fig. 6.

Praeglobotruncana helvetica (Bolli). Robaszynski and Caron, 1979, p. 39-42, pl. 46, figs. 1a-c, 2a-c.

Helvetoglobotruncana helvetica (Bolli). Wonders, 1980, p. 117, pl. 3, fig. 2a-c; Caron, 1985, p. 60, figs. 30-7, 8a-c; Loeblich and Tappan, 1988, p. 463-464, pl. 498, figs. 4-7.

Remarks.—Poorly preserved specimens of this species were obtained from only one horizon. Nevertheless, the figured specimen is identified as *H. helvetica* on the basis of its asymmetrical planoconvex lateral view, thick single keel that is shifted toward the spiral side, and staircase-like imbricate structures on the spiral side. This species is very rare in the area of study; however, it is quite important for interregional correlation.

Material.—Hypotype IGPS No. 102517.

Locality and horizon.—The figured specimen is from sample SRN-101, middle part of the Takinosawa Formation, middle Turonian.

Subfamily incertae sedis

Genus *Dicarinella* Porthault, 1970

***Dicarinella hagni* (Scheibnerova, 1962)**

Figure 7-5

Praeglobotruncana hagni Scheibnerova, 1962, p. 219, figs. 6a-c.

Praeglobotruncana sp. cf. *P. hagni* Scheibnerova. Butt, 1966, p. 174, figs. 2a-c (not 1a-c, 3a-4c).

Globotruncana kupperi Thalmann. Marianos and Zingula, 1966, p. 340-341, pl. 39, figs. 6a-c.

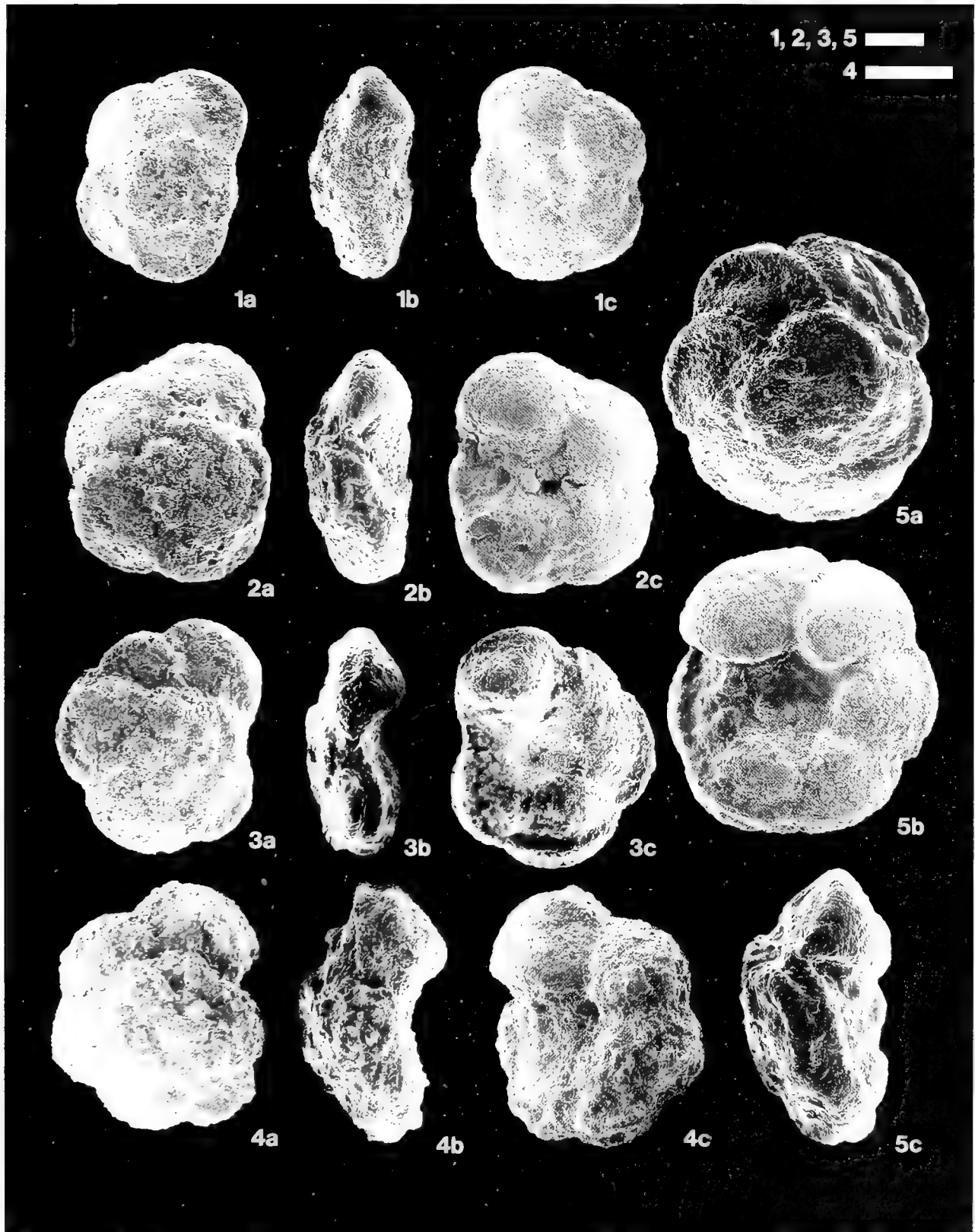
Dicarinella hagni (Scheibnerova). Robaszynski and Caron, 1979, p. 79-86, pl. 56, figs. 1a-c, 2a-c, pl. 57, figs. 1a-c, 2a-d; Caron, 1985, p. 45, figs. 18-2a-c, 3a-c.

Remarks.—This species differs from *Dicarinella roddai* in having chambers which increase their size more gradually and in having a greater number of chambers in the last whorl.

Material.—Hypotype IGPS No. 102509.

Locality and horizon.—The figured specimen is from sample SRN-034, middle part of the Takinosawa Formation,

Figure 7. 1-3. *Dicarinella roddai* (Marianos and Zingula). 1. IGPS No. 102520, sample loc. no. SRN-220, lower part of the Takinosawa Formation, uppermost Cenomanian. 2. IGPS No. 102511, sample loc. no. SRN 132, lower-middle part of the Takinosawa Formation, lower Turonian. 3. IGPS No. 102512, sample loc. no. SRN 034, middle part of the Takinosawa Formation, middle Turonian. 4. *Dicarinella imbricata* (Mornod), IGPS No. 102510, sample loc. no. SRN 034, middle part of the Takinosawa Formation, middle Turonian. 5. *Dicarinella hagni* (Scheibnerova), IGPS No. 102509, sample loc. no. SRN-034, middle part of the Takinosawa Formation, middle Turonian. Scale bars=100 μ m.



middle Turonian.

***Dicarinella imbricata* (Mornod, 1950)**

Figure 7-4

Globotruncana (Globotruncana) imbricata Mornod, 1950, p. 589-590, figs. 5 (III a-d).

Dicarinella imbricata (Mornod). Robaszynski and Caron, 1979, p. 87-92, pl. 58, figs. 1a-c, 2a-d, pl. 59, figs. 1a-c, 2a-c; Caron, 1985, p. 45, figs. 18-4a-c, 5a-c.

Remarks.—This species is easily distinguished from other species by its diagnostic stair-like imbrication of chambers on the dorsal side.

Material.—Hypotype IGPS No. 102510.

Locality and horizon.—The figured specimen is from sample SRN-034, middle part of the Takinosawa Formation, middle Turonian.

***Dicarinella roddai* (Marianos and Zingula, 1966)**

Figures 7-1-3

Globotruncana roddai Marianos and Zingula, 1966, p. 340, pl. 39, 5a-c.

non *praeglobotruncana roddai* (Marianos and Zingula). Douglas, 1969, p. 171-172, pl. 2, 2a-c.

Description.—Test medium to large in size, initially a low to medium-height trochospire, equatorial periphery slightly lobulate; chambers dorsally semicircular, ventrally trapezoidal in shape, somewhat inflated on ventral side, about 9 to 11 chambers in all arranged into 2 to 2.5 whorls, enlarging gradually in size as added, last 4 chambers almost similar in size, 5 slightly imbricated chambers in final whorl, with distinct double peripheral keels; sutures on dorsal side curved, raised with a keel which continues to one of double peripheral keels, ventrally radial, depressed, occasionally slightly raised; umbilicus shallow, its width about 1/4 of maximum diameter of test; primary aperture bordered by distinct, narrow- to medium-width lip, interiomarginal, umbilical-extraumbilical extending nearly to periphery; wall calcareous, weakly pustulated on earlier chambers.

Discussion.—This species resembles *Dicarinella hagni* but is distinguished by having less inflated chambers on ventral side, fewer and slightly imbricated chambers. Although Takayanagi (1965) described this species as *Globotruncana marginata*, Jirová's neotype figures of *G. marginata*, (Jirová, 1956, p. 253, figs. 1a-c) and one of the figured specimens of Reuss's syntypes which was later selected as the lectotype by Bolli *et al.* (1957) (Jirová's neotype has priority) are apparently different from Takayanagi's (1965, figs. 3a-c, 4a-c)

figures in having more chambers in the last whorl which are more globular and inflated, more gradually increasing in size as added, equatorial periphery more lobulate, narrower spaced keels, and a wider umbilicus. Marianos and Zingula (1966) stated that *D. roddai* (originally described as *Globotruncana roddai*) was a good marker for the lower Turonian in the type locality of this species, however, the stratigraphic distribution of this species in the area of study is restricted to the uppermost Cenomanian to lower part of the middle Turonian (Figure 3). In this stratigraphic range, this species occurs commonly. Therefore, it may be a useful supplemental species to locate the interval of the Cenomanian/Turonian boundary in Japan.

Material.—Hypotype IGPS No. 102520, 102511, 102512.

Locality and horizon.—The specimen IGPS No. 102520 is from SRN-220, lower part of the Takinosawa Formation, upper Cenomanian. IGPS No. 102511 is from sample SRN-132, lower-middle part of the Takinosawa Formation, middle Turonian. IGPS No. 102512 is from sample SRN-034, middle part of the Takinosawa Formation, middle Turonian.

***Dicarinella takayanagii* sp. nov.**

Figures 8-1-4

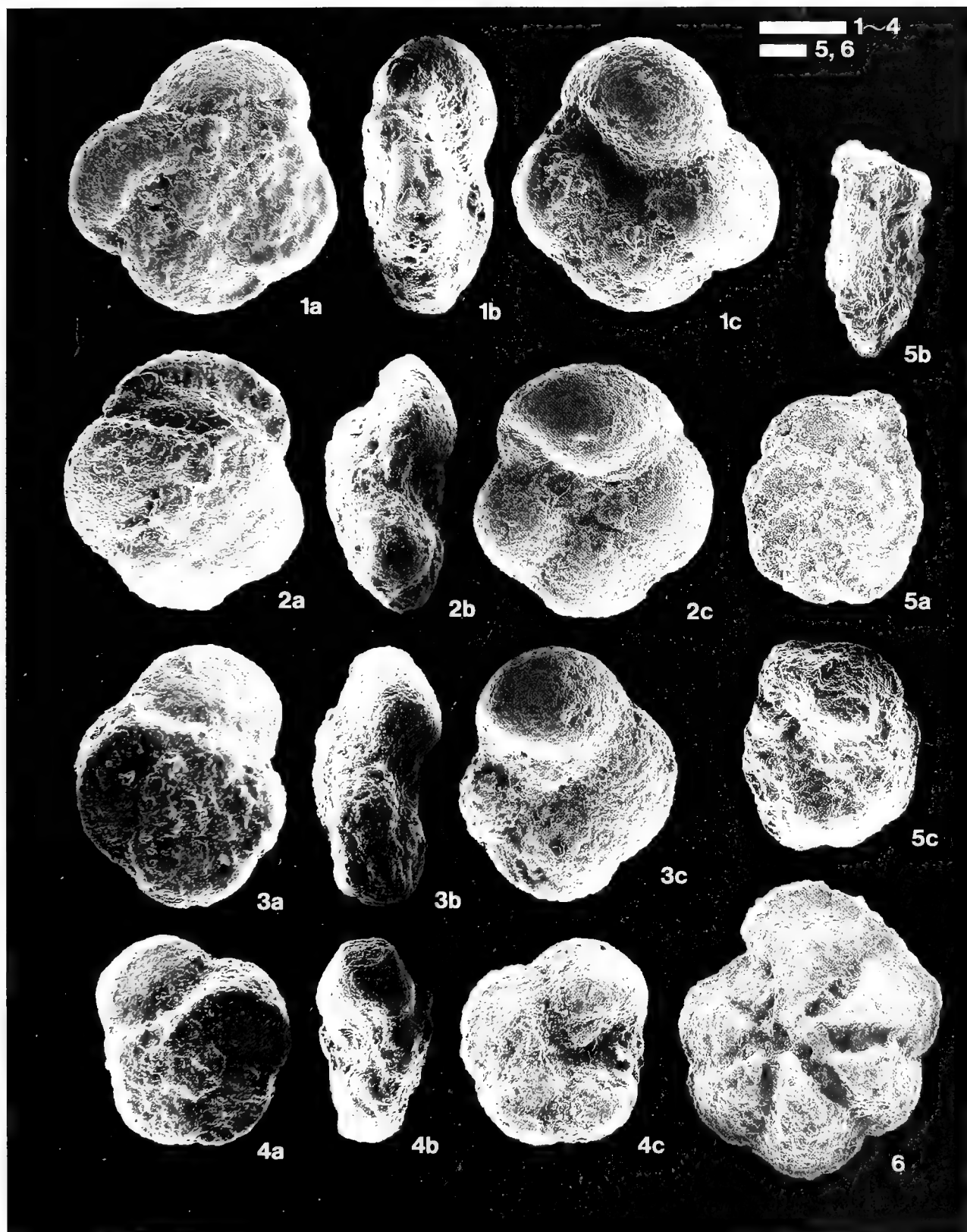
Diagnosis.—A low trochospiral species of *Dicarinella* with wedge-shaped chambers in last whorl and small umbilicus.

Description.—Test of medium to large size, low trochospiral, equatorial periphery lobulate; chambers initially globigerine-like, later ones becoming wedge-shaped and flat on dorsal side, triangular and inflated in shape on ventral side, about 10 chambers in all, enlarging rapidly in size as added, about 4.5 chambers in last whorl, with widely separated weak double peripheral keels, one of which is shifted toward spiral side; final chamber obliquely shifted toward umbilical direction, as a result, keels being discontinuous to final chamber; final chamber diagnostically elongated in spiral direction, occasionally lacking peripheral keels; sutures on dorsal side gently curved, raised with keels that are continuous to one of peripheral keels, sutures on ventral side radial and depressed; umbilicus shallow and narrow, its width about 1/4 of maximum diameter of test; primary aperture bordered by a distinct lip, interiomarginal, umbilical-extraumbilical; wall calcareous, earlier chambers weakly pustulated.

Remarks.—This species is distinguished from other species of *Dicarinella* in possessing wedge-shaped chambers in the last whorl on the dorsal side, spirally elongated final chamber and a narrower umbilicus.

Etymology.—In honor of Prof. Emeritus Y. Takayanagi in recognition of his contribution to the study of Cretaceous

Figure 8. 1-4. *Dicarinella takayanagii* sp. nov. 1. Paratype, IGPS No. 102513, sample loc. no. SRN-223, lower part of the Takinosawa Formation, uppermost Cenomanian. 2. Paratype, IGPS No. 102514, sample loc. no. SRN-223, lower part of the Takinosawa Formation, uppermost Cenomanian. 3. Holotype, IGPS No. 102515, sample loc. no. SRN-223, lower part of the Takinosawa Formation, uppermost Cenomanian. 4. Paratype, IGPS No. 102516, sample loc. no. SRN-223, lower part of the Takinosawa Formation, uppermost Cenomanian. 5. *Rotalipora deeckeii* (Franke), IGPS No. 102519, sample loc. no. KMZ-002, the uppermost part of the Hikagenosawa Formation, upper Cenomanian. 6. *Rotalipora cushmani* (Morrow), IGPS No. 102472, sample loc. no. SRN-220 (last occurrence horizon of *R. cushmani*), lower part of the Takinosawa Formation, uppermost Cenomanian. Same specimen as that shown in Hasegawa and Saito (1993). Scale bars=100 μ m.



foraminifera in Japan.

Material.—Holotype IGPS No. 102515; paratypes IGPS No. 102513, 102514, 102516.

Dimensions.—Maximum diameter of holotype 0.29 mm, maximum thickness 0.17 mm.

Type locality and horizon.—The holotype and all paratypes are from sample SRN-223 (43°2.60'N, 142°9.73'E), lower part of the Takinosawa Formation, uppermost Cenomanian.

Family Rotaliporidae Sigal, 1958
Subfamily Rotaliporinae Sigal, 1958
Genus *Rotalipora* Brotzen, 1942

***Rotalipora cushmani* (Morrow, 1934)**

Figures 8-6; 9-4

Globorotalia cushmani Morrow, 1934, p. 199, pl. 31, fig. 4a-b.

Rotalipora cushmani (Morrow). Loeblich and Tappan, 1961, p. 297-298, pl. 8, figs. 1-8, 10 (not fig. 9); Pessagno, 1967, p. 292-293, pl. 51, figs. 6-9; Robaszynski and Caron, 1979, p. 69-74, pl. 7, figs. 1a-c, pl. 8, figs. 1a-c, 2a-c; Wonders, 1980, p. 125-126, pl. 3, fig. 3a-c; Caron, p. 69, figs. 31-8-11.

Remarks.—This species is distinguished from other species of *Rotalipora* by having a lobulated periphery, semi-circular chambers ornamented by pustules in the last whorl, pronounced supplementary apertures with developed lips. The last occurrence of this species corresponds to that of the genus *Rotalipora* in this study. This species is a very important index in Japan for interregional correlation.

Material.—Hypotypes IGPS No. 102471, 102472.

Locality and horizon.—Two figured specimens are from SRN-220 (last occurrence horizon of *R. cushmani*), lower part of the Takinosawa Formation, uppermost Cenomanian.

***Rotalipora deecke* (Franke, 1925)**

Figure 8-5

Rotalia deecke Franke, 1925, p. 88, 90, pl. 8, figs. 7a-c (This inaccessible literature is indirectly accessible from "Ellis and Messina, 1940 et seq., Catalogue of Foraminifera").

Rotalipora deecke (Franke). Robaszynski and Caron, 1979, p. 75-80, pl. 9, figs. 1a-2c, pl. 10, 1a-2c.

Remarks.—This species is very similar to *Rotalipora reicheli*, but differs in having periumbilical ridges extended from raised sutures on the ventral side and narrower umbilicus.

Material.—Hypotype IGPS No. 102519.

Locality and horizon.—The figured specimen is from KMZ-002, uppermost part of the Hikagenosawa Formation, upper

Cenomanian.

***Rotalipora* sp. aff. *R. gandolfii* Luterbacher and Premoli-Silva, 1962**

Figure 9-3

Remarks.—This species resembles *Rotalipora gandolfii*, but differs in having the hemispherical last two chambers. This morphological feature is rather reminiscent of *Rotalipora cushmani*.

Material.—Hypotype IGPS No. 102524.

Locality and horizon.—The specimen IGPS No. 102524 is from SSS-020, lowermost part of the Takinosawa Formation, upper Cenomanian.

***Rotalipora greenhornensis* (Morrow, 1934)**

Figure 9-5

Globorotalia greenhornensis Morrow, 1934, p. 199, pl. 31, figs. 1a-c.

Rotalipora greenhornensis (Morrow). Loeblich and Tappan, 1961, p. 299-301, pl. 7, figs. 5-10; Pessagno, 1967, p. 295-297, pl. 50, fig. 3, pl. 51, figs. 15-17, 19-21 (not figs. 13, 14, 18); Pessagno, 1967, p. 289-292, pl. 50, figs. 4-6; Robaszynski and Caron, 1979, p. 85-90, pl. 12, figs. 1a-c, 2a-c, pl. 13, figs. 1a-c, 2a-c; Caron, 1985, p. 69, text-figs. 32-1, 2.

Remarks.—This species is easily distinguished from other species of *Rotalipora* by having greater number of chambers in the last whorl and crescent-shaped chambers which are often concave on the dorsal side. The last occurrence of this species is at the same stratigraphic horizon as that of *Rotalipora cushmani* in the area of study.

Material.—Hypotype IGPS No. 102473.

Locality and horizon.—The figured specimen is from SRN-220, lower part of the Takinosawa Formation, uppermost Cenomanian.

Subfamily Globotruncaninae Brotzen, 1942
Genus *Marginotruncana* Hofker, 1956

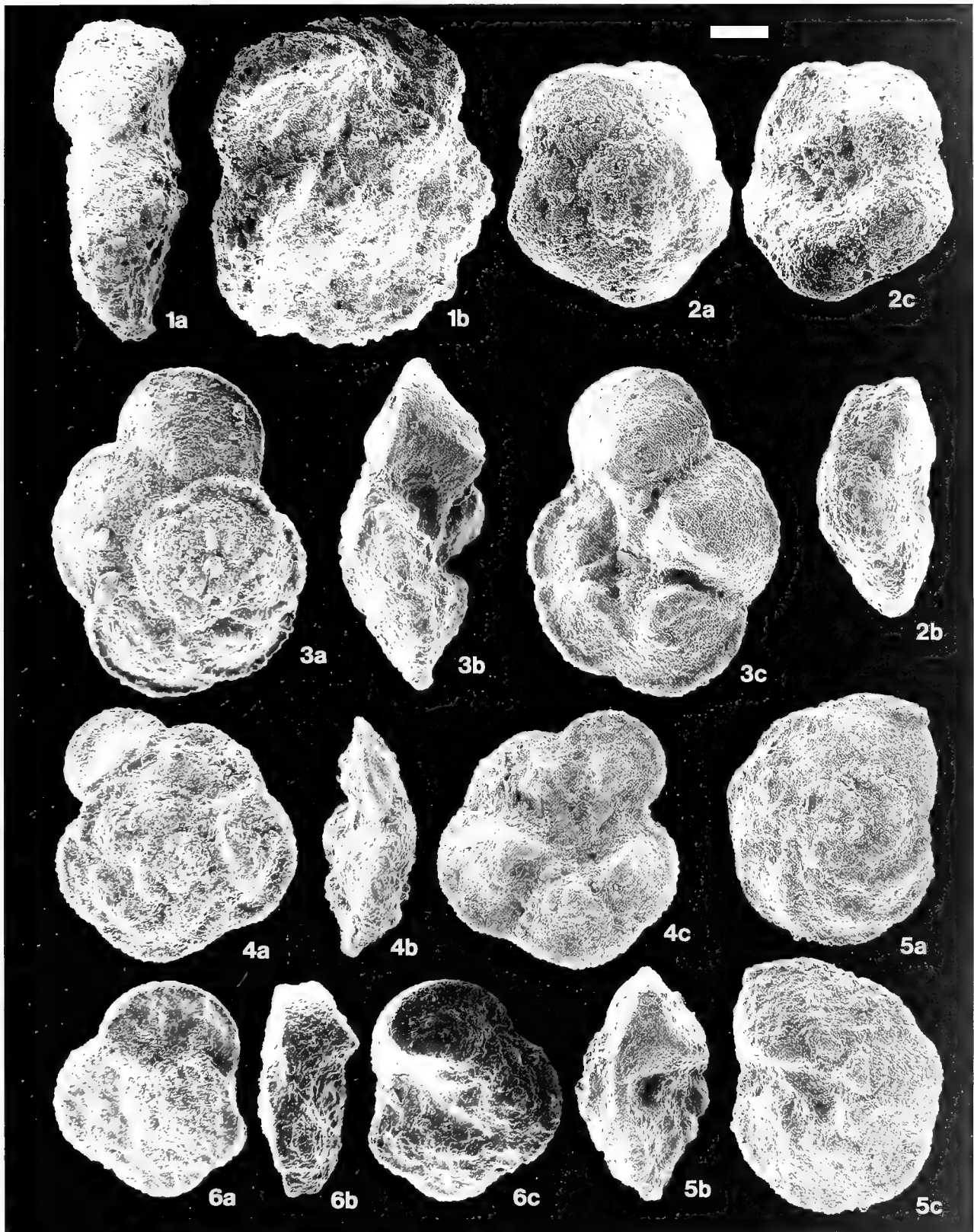
***Marginotruncana pseudolinneiana* Pessagno, 1967**

Figure 9-6

Marginotruncana pseudolinneiana Pessagno, 1967, p. 310, pl. 65, figs. 24-27; Robaszynski and Caron, 1979, p. 123-128, pl. 67, 1a-2d, pl. 68, 1a-2c; Caron, 1985, p. 61, text-figs. 26-7, 8.

Remarks.—This species is easily distinguished from other

Figure 9. 1. *Helvetoglobotruncana helvetica* (Bolli), IGPS No. 102517, sample loc. no. SRN-101, middle part of the Takinosawa Formation, middle Turonian. 2. *Marginotruncana schneegansi* (Sigal), IGPS No. 102521, sample loc. no. SRN-132, lower-middle part of the Takinosawa Formation, lower Turonian. 3. *Rotalipora* sp. aff. *R. gandolfii* Luterbacher and Premoli-Silva, IGPS No. 102524, sample loc. no. SSS-020, lowermost part of the Takinosawa Formation, upper Cenomanian. 4. *Rotalipora cushmani* (Morrow), IGPS No. 102471, sample loc. no. SRN-220 (last occurrence horizon of *R. cushmani*), lower part of the Takinosawa Formation, uppermost Cenomanian. Same specimen as that shown in Hasegawa and Saito (1993). 5. *Rotalipora greenhornensis* (Morrow), IGPS No. 102473, sample loc. no. SRN-220, lower part of the Takinosawa Formation, uppermost Cenomanian. Same specimen as that shown in Hasegawa and Saito (1993). 6. *Marginotruncana pseudolinneiana* Pessagno, IGPS No. 102522, sample loc. no. SRN-062, lower part of the Shirogane Formation, upper Turonian. Scale bar = 100 μ m.



species by its diagnostically rectangular shape in lateral view. This species characterizes the middle Turonian to Coniacian interval in Japan.

Material.—Hypotype IGPS. No. 102522.

Locality and horizon.—The figured specimen is from SRN-062, lower part of the Shirogane Formation, upper Turonian.

Marginotruncana schneegansi (Sigal, 1952)

Figure 9-2

Globotruncana schneegansi Sigal, 1952, p. 33, text-fig. 34.

Marginotruncana schneegansi (Sigal). Robaszynski and Caron, 1979, p. 135-140, pl. 70, fig. 1a-2e, Pl. 71, 1a-2d; Caron, 1985, p. 61, text-figs. 27, 3-6.

Remarks.—The first occurrence of this species characterizes the lower Turonian in Japan.

Material.—Hypotype IGPS No. 102521.

Locality and horizon.—The figured specimen is from SRN-132, lower-middle part of the Takinosawa Formation, lower Turonian.

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Tidal growth patterns and growth curves of the Miocene potamidid gastropod *Vicarya yokoyamai*

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Abstract. Continuous growth sequences are recorded in vertical (= median longitudinal) sections of the columella of the fossil potamidid gastropod *Vicarya yokoyamai* Takeyama, from subtropical Miocene faunas of Japan. Shells from the Mizunami, Uchiura, Bihoku, and Masuda groups show semidiurnal tidal growth patterns. This suggests that *V. yokoyamai* lived in the intertidal zone. Growth curves were reconstructed on the basis of numbers of tidal growth lines. These growth curves were found to be very similar with one another, and indicated that shell-height increased from 1.5 cm to 8 cm in two years.

Key words : columella, growth rate, intertidal, micro-growth increment, micro-growth line, tide

Introduction

Invertebrate hard parts such as molluscan shells and coral skeletons grow incrementally, forming alternating sequences of micro-growth lines and micro-growth increments that constitute their micro-growth patterns. Micro-growth patterns reflect physiological and environmental changes that occurred during their formation. Reconstruction of these changes from micro-growth patterns observed in the hard parts of a variety of organisms has been attempted in many studies (e.g. Wells, 1963 ; Berry and Barker, 1968 ; House and Farrow, 1968 ; Pannella and MacClintock, 1968 ; Pannella *et al.*, 1968 ; Dolman, 1975 ; Scrutton, 1978 ; Lutz and Rhoads, 1980 among others).

Intertidal organisms such as bivalves, gastropods, and barnacles record the effects of changing tides, as exposure and immersion are commonly reflected in their micro-growth patterns (Evans, 1972 ; Bourget and Crisp, 1975 ; Crisp and Richardson, 1975 ; Richardson *et al.*, 1979, 1980a, 1980b, 1981 ; Richardson *et al.*, 1980c ; Ekarante and Crisp, 1982 ; Ohno and Takenouchi, 1984 ; Ohno, 1984, 1985, 1989 ; Richardson, 1987, 1988a, 1988b ; Tojo and Ohno, 1999). Using these records, ancient tidal periods and tidal patterns have been reconstructed from fossil bivalves (Ohno, 1984, 1989 ; Tojo *et al.*, 1999). Tidal growth patterns are also a suitable index for the time scale of growth, so they can be used to reconstruct the growth rates of hard parts (Richardson, 1987 ; Tojo and Ohno, 1999). Previous studies of growth rates are based in many cases on annual rings that were recognized by comparative analysis of growth lines and oxygen isotopes of the shells (Jones *et al.*, 1978 ; Jones, 1980 ; Thompson *et al.*, 1980 ; Jones, 1981), but many gastropods have no obvious yearly rings. Thus we attempt the reconstruction of growth

curves from tidal growth patterns.

Few studies of micro-growth patterns in gastropod shells have been undertaken, because coiling of the gastropod shell obstructs the collection of continuous growth sequences spanning the whorls. However, Tojo and Ohno (1999) have proposed an easy method to obtain a continuous micro-growth pattern from one whorl to the next in the Recent potamidid gastropod *Terebralia palustris* (Linnaeus), using sections of the columella. This method made it easy to access records of gastropod growth. Tojo and Ohno (1999) observed tidal growth patterns in shells of *T. palustris*. They inferred that one micro-growth line corresponds to a 12.4 hour interval of low tides and reconstructed the growth curve of an individual *T. palustris* shell. This growth curve was consistent with one that had been reconstructed from a population analysis. Analysis of micro-growth patterns by this method permits the reconstruction of changing growth rates even from a single fossil specimen or species known only from small populations.

The fossil potamidid gastropod *Vicarya* has been regarded as a characteristic element of warm-water faunas from Eocene to Miocene in age. Tojo and Sakakura (1998) reported tidal growth patterns in shells of *Vicarya yokoyamai* from the Mizunami Group. However, little is known of the growth of *Vicarya* because it is an extinct genus.

The method of Tojo and Ohno (1999) can be applied to shells of *V. yokoyamai*. We observed tidal growth patterns in shells of *V. yokoyamai* from four localities (Figure 1) and reconstructed their growth curves.

Material

In this study, we used fragments of *V. yokoyamai* from

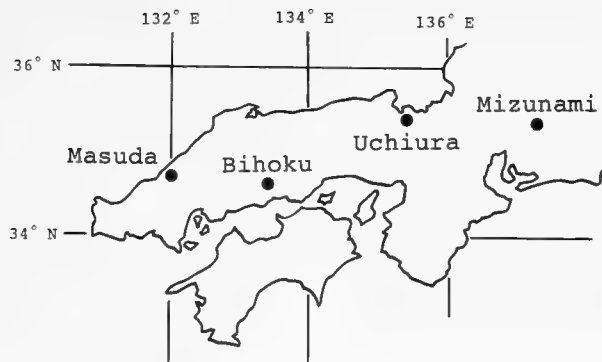


Figure 1. Locality map for *Vicarya yokoyamai* specimens utilized in this study.

subtropical tidal or shallow marine facies of Miocene age in Japan. To reconstruct the growth curve of *V. yokoyamai* (Figure 2A), we used a total of six specimens, three from the Mizunami Group in Gifu Prefecture, and one each from the Uchiura Group in Kyoto Prefecture, the Bihoku Group in Okayama Prefecture, and the Masuda Group in Shimane Prefecture (Figure 1). In the following discussion, specimens are referred to by the group name, and the three specimens from the Mizunami Group are called Mizunami A, B and C. Two species names that had been established, *V. yokoyamai* and *Vicarya japonica*, were synonymized by Kanno (1986).

Preparation for columella method

In order to prepare vertical (=median longitudinal) and horizontal (=cross) sections of the gastropod shell, samples were cut and ground with a graded series of carborundum and polished with diamond paste. A binocular microscope and a scanning electron microscope (SEM) were used for observation of shell micro-growth patterns (Figure 2B). For observation with the SEM, polished samples were etched with 0.5 mol/l HCl and then coated with gold.

Results

Micro growth pattern

Micro-growth pattern consists of two components of growth layers, micro-growth lines and micro-growth increments. Micro-growth lines are the layers which are relatively resistant to etching. Thus, they are observed as lineridges under SEM. Micro-growth increments are the layers between micro-growth lines. Micro-growth lines show various thicknesses, but are generally thinner than micro-growth increments.

Micro-growth lines of *V. yokoyamai* appear as relatively light layers under the binocular microscope (Figures 2B, D).

Formation of columella

Before observing the columella sections, we examined the outer shape of the columella to understand its formation (Figure 2C). The basal part of the columella has a trough-like structure along its coiling axis. One flank of the trough continues to the outer lip; the other covers the bottom of the preexisting whorl (Figure 2C). During growth of the shell, the trough extends downwards (abapically) in the direction of coiling, the apical end being filled with new shell material. The formation of new growth layers over this surface results in the formation of the columella.

Growth layers at the bottom of the trough contribute to growth of the central part of the columella, and those on the preexisting outer surface of the neck contribute to growth of the columella rim and a part of a whorl. This layer becomes part of the "ceiling" of the new shell whorl. The new shell is laid down directly upon that formed in the previous whorl. This surface of contact appears as a line in shell sections that is referred to as the "borderline" (Figures 2B, D; Tojo and Ohno, 1999).

Appearance of the growth layers in sections

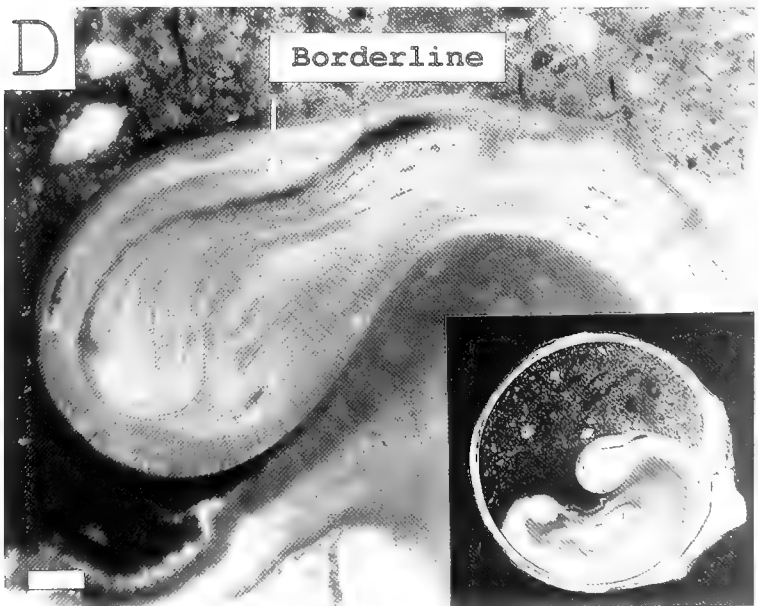
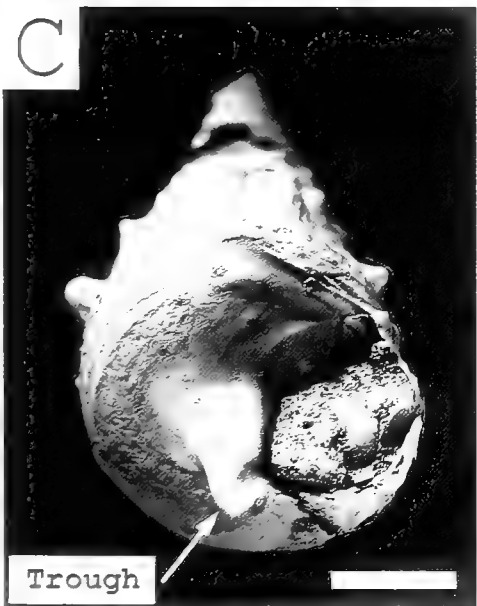
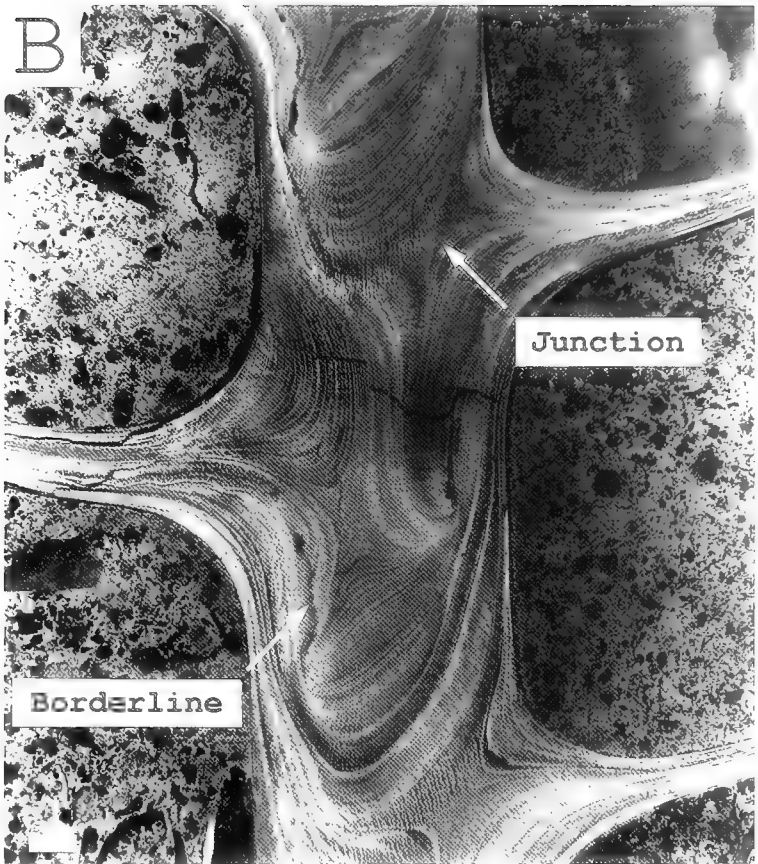
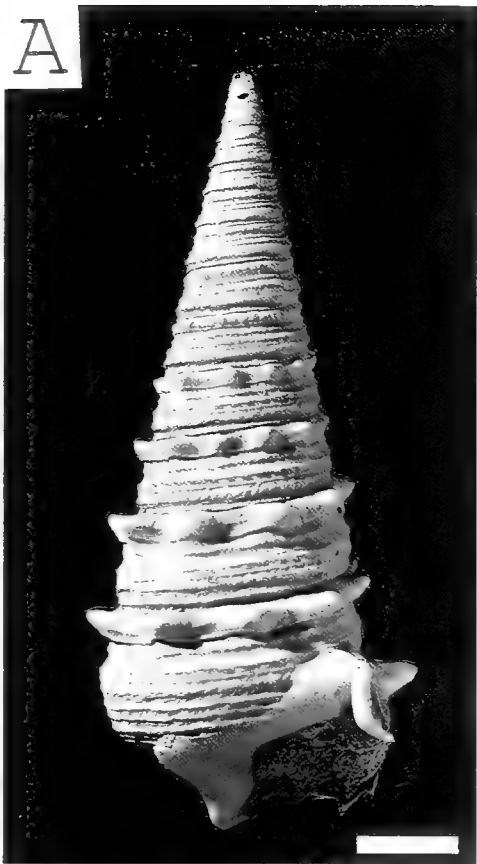
In vertical (=median longitudinal) section, each whorl shows a pair of more or less hyperbolic patterns, alternately on the right and left sides of the coiling axis (Figures 2B, 3). One is the trace of the trough facing the observer, and the other is that of the trough opposing the observer. The center of this hyperbolic pattern is called the "junction" (Figure 2B; Tojo and Ohno, 1999). The shell of the columella between successive junctions on the same side of the coiling axis corresponds to the growth record of one shell whorl. Borderlines are also observed in vertical sections (Figure 2B).

Continuous growth sequence on the vertical shell section

Correlation of the growth layers was accomplished by tracing them on vertical (=median longitudinal) and horizontal (=cross) sections. First a vertical section was made and the growth layers on it were documented (Figure 2B). Then the two halves of the shell were glued together with adhesive. The "repaired shell" was then cut horizontally. The cut surface was polished and its growth layers were documented (Figure 2D). Then the surface was ground away until shell corresponding to 90° of coiling had been removed. Polishing and documentation of horizontal sections at 90° intervals was repeated for more than one full whorl of the shell (Figure 3).

The columella occupies the center of the cross section,

Figure 2. A. A shell of *Vicarya yokoyamai* Takeyama, Middle Miocene, Mizunami Group, Gifu Pref. The scale bar is 1cm long. B. A vertical section of *Vicarya yokoyamai*, Middle Miocene, Mizunami Group, Gifu Pref. Along the coiling axis, micro growth lines and intervening micro growth increments are observed. The scale bar is 1mm long. C. The basal part of columella of *Vicarya yokoyamai*, Middle Miocene, Mizunami Group, Gifu Pref. The trough running along the columella and the new shell layer covering the previous whorl surface can be seen. The scale bar is 1cm long. D. A horizontal section of *Vicarya yokoyamai* with the columella at the center, Middle Miocene, Mizunami Group, Gifu Pref. The scale bar is 1mm long. (Photomicrographs of sections taken with binocular microscope.)



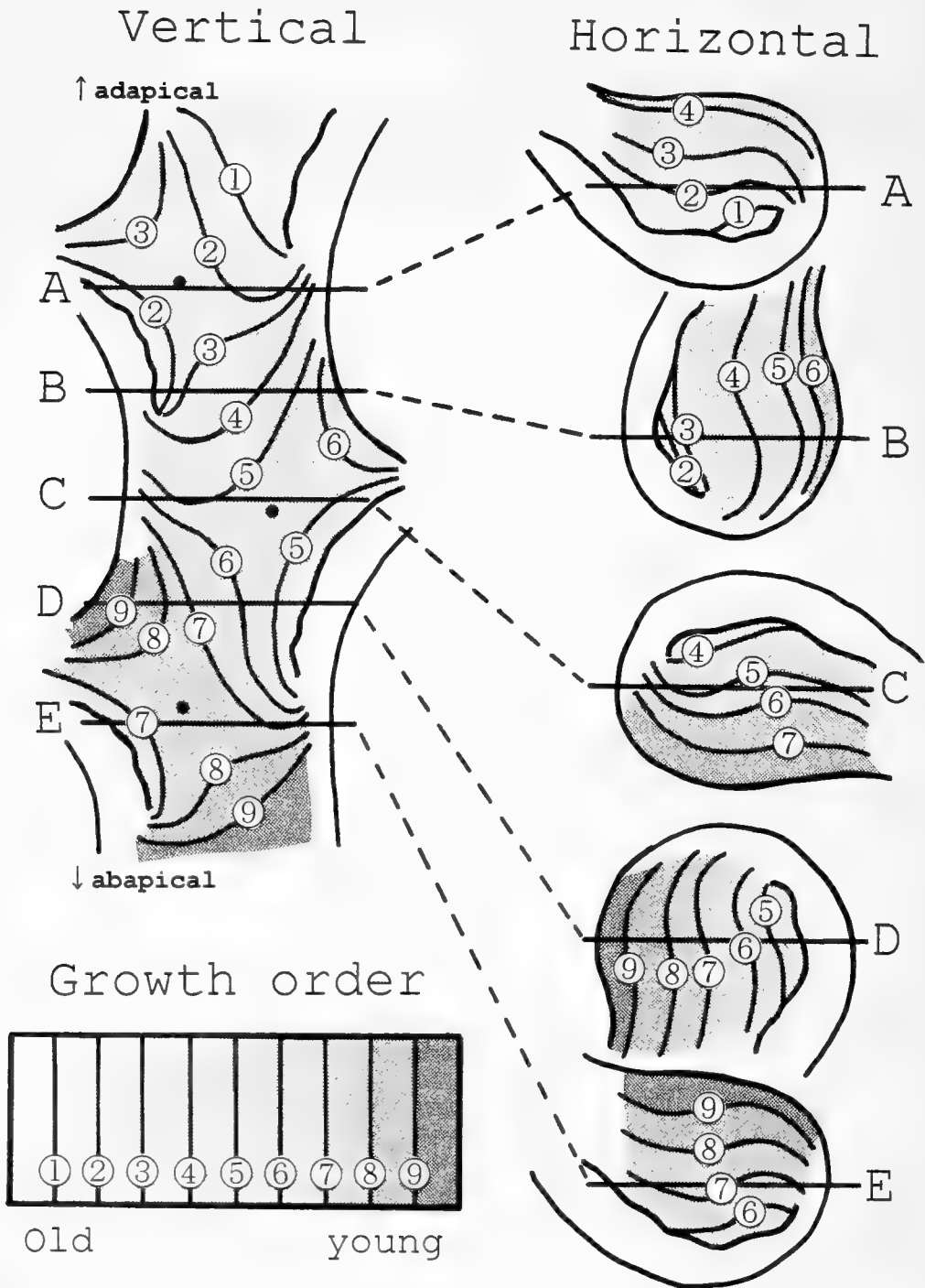


Figure 3. Correlation of growth layers on vertical (=median longitudinal) sections and horizontal (=cross) sections. Growth layers are numbered in temporal order from 1 to 9. Lines A to E show the correspondence of vertical and horizontal sections. On vertical section dots show junctions.

with a portion of the whorl extending away from it as if it were a vortex (Figure 2D). One side of the link between the columella and the vortex forms a concave surface and the other side is convex. The concave surface is underlain by

an accumulation of numerous U-shaped layers. In successive horizontal sections, viewed abapically, the vortex rotates clockwise. New growth layers are added to the surface of the concave side, move to the convex side abapically, and

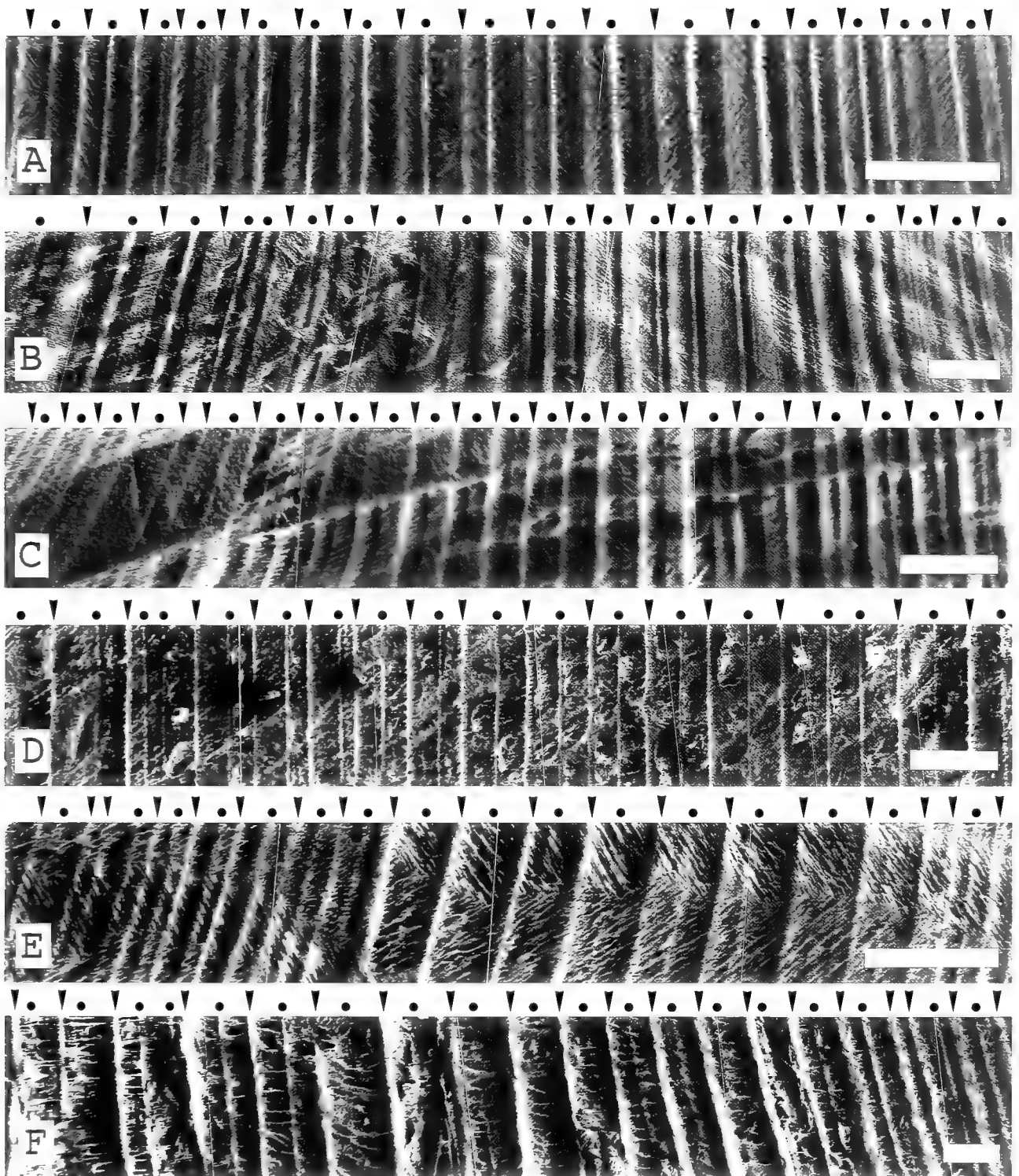


Figure 4. Tidal growth patterns recorded in the columella sections of *Vicarya yokoyamai*. **A.** Mizunami A specimen. **B.** Mizunami B specimen. **C.** Mizunami C specimen. **D.** Uchiura specimen. **E.** Bihoku specimen. **F.** Masuda specimen. Continuous semidiurnal tidal growth patterns are indicated by the alternation of thicker (arrowhead) and thinner (dot) micro growth lines. The order of micro growth line thickness changes. All scale bars represent 100 μm. (Photomicrographs taken with SEM.)

finally vanish.

Through observation of successive horizontal sections at 90° intervals the growth layers could be examined and numbered. In Figure 3 (right) the stack of numerous U-shaped growth layers is shown diagrammatically. Only lines with characteristic features, which could easily be correlated in vertical and horizontal sections, were numbered; the oldest conspicuous growth layer was numbered 1 and the newest numbered 9. All the corresponding growth layers could be seen on the vertical section for this growth interval, corresponding to more than one shell whorl (Figure 3 left). Since the mode of growth of the *V. yokoyamai* shell does not change during its ontogeny, all visible growth layers can be recognized and counted on the median longitudinal section of the shell.

Tidal growth patterns

Vicarya yokoyamai shells from the four localities show two sorts of accretionary patterns of micro-growth lines on the columella (Figure 4). One is the alternation of thicker (indicated by arrowheads in Figure 4) and thinner (dots in Figure 4) micro-growth lines. The other is an inversion of the arrangement of thicker and thinner micro-growth lines at approximately every 28.5 growth lines. The same micro-growth patterns of *V. yokoyamai* were reported in specimens from the Mizunami Group by Tojo and Sakakura (1998). These are characteristic features of tidal growth patterns (Dolman, 1975; Richardson *et al.*, 1979, 1980a, 1981; Richardson, 1988b; Ohno, 1989).

Identical alternations and inversions are reported from intertidal bivalves (Richardson *et al.*, 1979, 1981; Ohno, 1984, 1989; Richardson, 1988b) and gastropods (Ohno and Takenouchi, 1984; Tojo and Ohno, 1999). In bivalve shells from semidiurnal, mesotidal regimes, the alternation of thicker and thinner micro-growth lines is caused by differences in temperature between daytime and nighttime exposures to the air (Richardson *et al.*, 1980a; Richardson 1988b; Ohno, 1989). Inversions in the order of thicker and thinner micro-growth lines result from the different periodicities of approximately semidiurnal tides and of the 24 hour cycle of day and night. The zone where the inversion occurs is called the "switch zone" (Ohno, 1989). This mechanism may be responsible for the alternations and inversions observed in the succession of micro-growth lines of *V. yokoyamai* (Figure 4) from the Middle Miocene. This result is compatible with the tidal growth patterns of fossil bivalves from the Mizunami Group recognized by Ohno (1989). The preservation of this micro-growth pattern in all specimens suggests that *V. yokoyamai* lived in the intertidal zone.

The relationship between the number of tidal emersions and micro-growth lines in intertidal bivalves and gastropods has been confirmed by several experiments (Richardson *et al.*, 1979, 1980a, 1980b; Richardson *et al.*, 1980c; Ekarante and Crisp, 1982; Ohno, 1983, 1985, 1989; Richardson, 1987, 1988a, 1988b). Hence, it is reasonable to infer that one micro-growth line in the shell of *V. yokoyamai* is formed in each tidal cycle.

Reconstruction of growth curves

A continuous growth record can be obtained from the vertical section of a columella (Figures 2, 3). If shell growth was semidiurnal in *V. yokoyamai*, it should be possible to reconstruct growth curves using these observations.

Height of shell

To reconstruct the growth curve of *V. yokoyamai*, we had to estimate the original height of the shell. However, all specimens had lost some part of the apical portion of the shell. We extrapolated to determine the original height from the angle defined by the whorls of the surviving shell (Figure 5).

Growth curves of Mizunami specimens

We counted the number of micro-growth lines and measured the shell height at which each junction between whorls of the Mizunami specimens was formed (hereafter called junction height: Figure 5). The shell between successive junctions on the same side of the coiling axis corresponds to the growth record of one shell whorl. Therefore, the number of micro-growth lines between successive junctions, multiplied by 12.4 hours, represents the

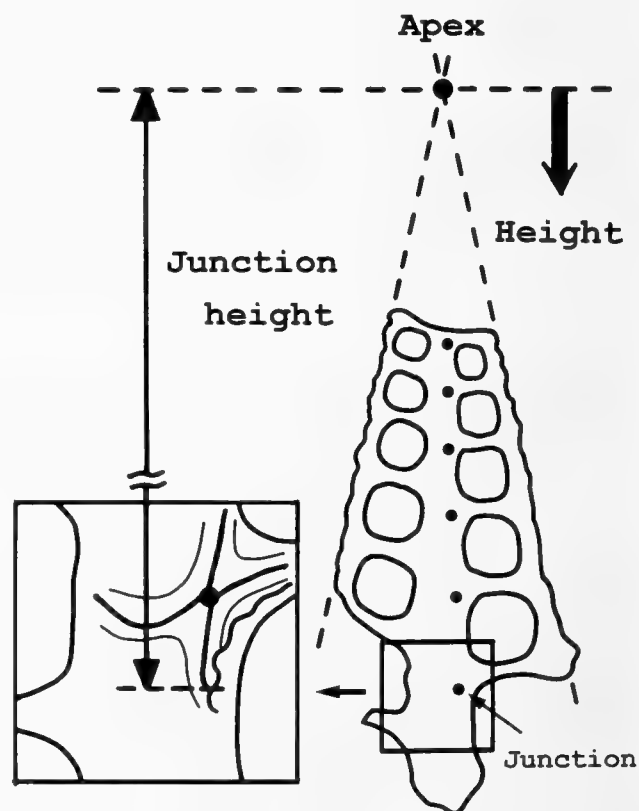


Figure 5. Shell height is the vertical distance between the tip of the columella and the reconstructed position of the apex, extrapolated from the outer surface of surviving shell whorls. Junction height is the shell height at which each junction was formed.

time required for growth of the shell whorl. Given the junction heights, we were able to reconstruct the growth curve.

First, the data for Mizunami C were plotted on a graph (Figure 6A). Then, data for Mizunami A and B were plotted as if their first junction heights lined up with that of Mizunami C (Figure 6A). The points plotted are based on the total number of clear micro-growth lines plus half the number of

unclear micro-growth lines. Error bars represent the accumulated number of unclear micro growth lines. This graph shows that the growth curves of Mizunami specimens are similar. The growth rate gradually decreased with growth.

Growth curves of other specimens

We counted the numbers of micro-growth lines and

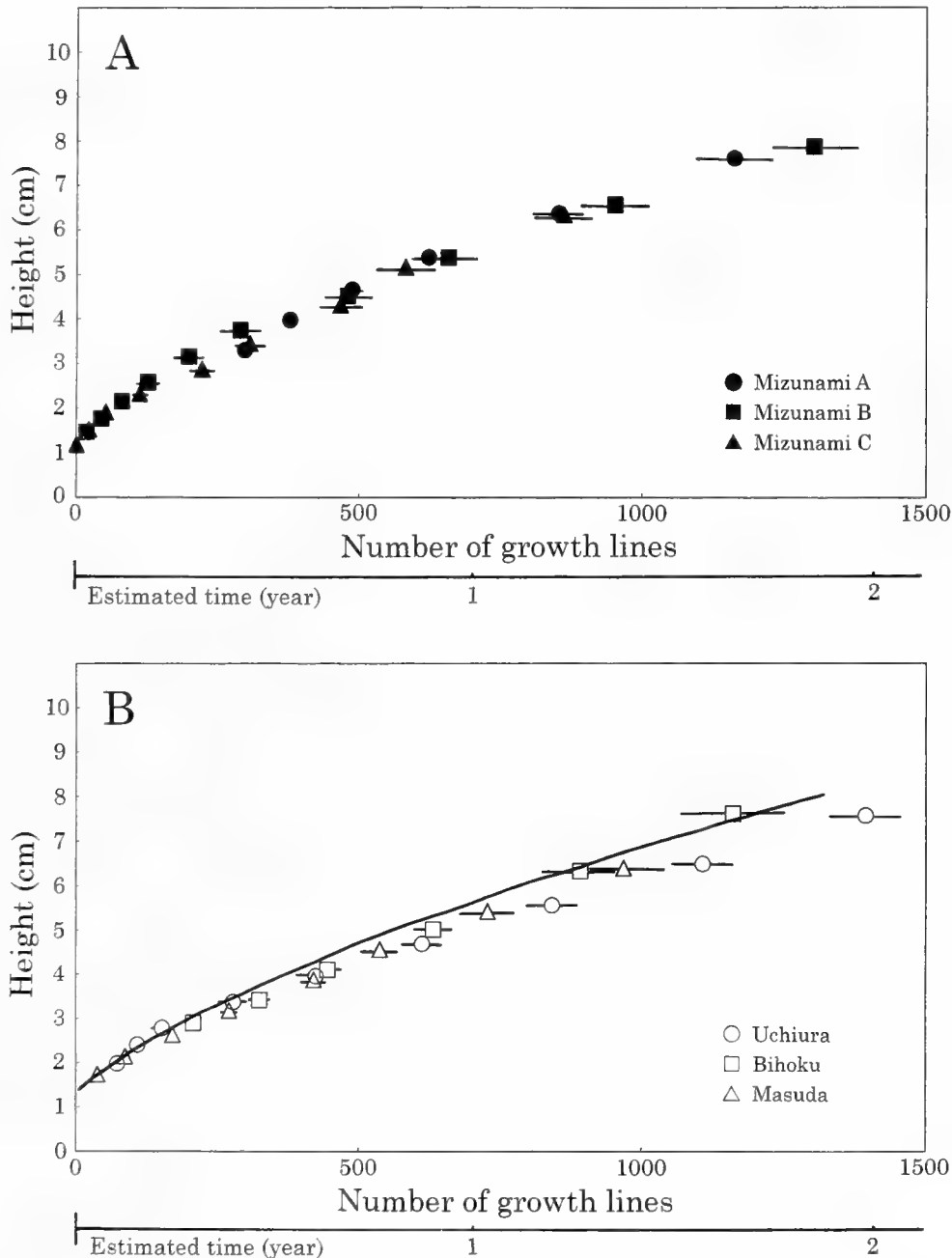


Figure 6. A. Reconstructed growth curves of *Vicarya yokoyamai* from the Mizunami specimens. B. Reconstructed growth curves of *Vicarya yokoyamai* from various areas. The solid line is the approximate growth curve of the Mizunami specimens.

measured the junction heights of other specimens, plotting similar growth curves (Figure 6B). In the figure, the solid line is the curve of best fit to the Mizunami specimen data. Data from other specimens were plotted so that their first junction heights lie on the Mizunami curve (Figure 6B). This graph shows that the growth curves of the Uchiura, Bihoku, and Masuda specimens are similar to those of shells from Mizunami.

Discussion

Previous studies have suggested that *Vicarya* lived in the intertidal zone of a subtropical mangrove swamp (Oyama, 1950; Chinzei, 1978; Itoigawa and Tsuda, 1986). This inference is corroborated by the pattern of tidal growth documented here. The alternation of thicker and thinner micro-growth lines is reported only from intertidal organisms. The observation of such alternations in all specimens suggests that *V. yokoyamai* lived in an intertidal zone where it was emersed twice a day.

Distinct major growth breaks, such as winter or spawning breaks, were not observed in this study. This is consistent with the subtropical habitat of *V. yokoyamai*, which lived during the warm Neogene climatic optimum (Chinzei, 1978; Chinzei, 1986; Ozawa *et al.*, 1995). Hence, there was no necessity for a winter break in growth.

We reconstructed the growth curves of six specimens from continuous growth records and the assumption that one micro-growth line formed in a tidal interval. Reconstructed growth curves approximate a logistic form. The logistic pattern of declining growth rate is typical of most invertebrates, indeed of most animals. This suggests the reconstruction is correct. The shells grew from 1.5 cm to 8 cm in height over two years. The adult shell of *Vicarya* has a prominent, thick outer lip. The growth curves suggest that these animals reached maturity and formed the prominent outer lip at the age of two years.

Jones (1981) showed that the standardized growth rate of *Spisula solidissima* changes drastically in conjunction with monthly average mean sea surface temperatures. The change of growth rate is largely explained by the presence of the winter break. In contrast to this cool-water species, the reconstructed growth curves of the *Vicarya* specimens show no or weak seasonal fluctuations. This suggests that *V. yokoyamai* grew in a stable subtropical environment without any climatic deterioration. This inference should be tested by studies of the growth of cooccurring fossils.

The number of specimens studied here is small, due to weathering and recrystallization of most specimens. However, the good agreement of the growth curves in shells from different formations and localities suggests that the columella-method and tidal growth analysis can be used to infer high-resolution population dynamics of fossil gastropod assemblages of various ages.

Conclusion

The columella method yields evidence of continuous growth sequences in shells of the fossil potamidid gastropod

V. yokoyamai. The tidal growth patterns of *V. yokoyamai* shells suggest that this gastropod lived in the intertidal zone, under the influence of semidiurnal tides. The reconstructed growth curves of specimens from the Mizunami, Uchiura, Bihoku, and Masuda groups show that their shells grew at similar rates, from 1.5 cm to 8 cm in height in two years.

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Ordovician cephalopods from the Maggol Formation of Korea

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Abstract. A cephalopod fauna consisting of 11 species belonging to 7 genera is described from the Lower Ordovician Maggol Formation near Taebaeg City in South Korea. The fauna includes two new species, *Ormoceras weoni* and *Michelinoceras cancellatum*, and *Wutinoceras*, a primitive genus of the family Actinoceratidae first reported from South Korea. *Ormoceras cricki* from the Middle Ordovician Duwibong Formation occurs in the uppermost horizon of the Maggol Formation, and thus may be regarded as a forerunner of the ormocerids in Korea.

The Maggolian cephalopod fauna comprising *Wutinoceras robustum*, *Kogenoceras nampiaoense*, and *Manchuroceras* spp. shows closest affinities with those from the Setul Limestone of the Langkawi Islands, Malaysia and from the Beianzhuang Formation of Hwangho Basin, North China. This fauna is, therefore, assigned in age to the late Ibexian to early Whiterockian in the American Early Ordovician scale.

Key words: cephalopod fauna, lower Whiterockian, Maggol Formation, Ormoceratidae, upper Ibexian, Korea

Introduction

Kobayashi (1927) first described seven cephalopod species from the Ordovician of South Korea, including *Kotoceras grabau* from the Middle Ordovician Maggol Formation. In a subsequent monograph (Kobayashi, 1934), the stratigraphic occurrences of these species were reassigned to the overlying Middle Ordovician Jigunsan Formation.

Cephalopod fossils seldom occur in the Maggol Formation. They are commonly found as partial phragmocones whose internal structures are difficult to recognize because of recrystallization. Despite such generally unfavorable fossil preservation, more than fifty well preserved cephalopod specimens have been recently collected from the Maggol Formation of Sanaegol, Taebaeg City, Kangweondo, Korea (Figure 1).

This paper describes the cephalopod fauna of the formation based mainly on newly collected material in addition to Kobayashi's (1927) type and figured specimens. Comparison with contemporary faunas from other regions is also given in this paper, with discussion of the biostratigraphic and paleobiogeographic implications of the Maggol fauna.

All specimens described herein are housed in the Department of Earth Science, Teachers College, Kyungpook National University (prefix KPE), Taegu, Korea.

Geological setting

The Maggol Formation was originally named by Kobayashi (1927) for a limestone formation "the Great Limestone Group"

exposed near the village "Maggol", at the Sangdong Scheelite Mine, Sangdong, Yeongweol. The formation extends from east to west in the southern limb region of the Baegunsan Syncline where the Duwibong type Joseon Supergroup is widely distributed. The formation ranges from 250 m to 400 m in thickness.

The Maggol Formation conformably overlies the Dumugol Formation and is overlain by the Jigunsan Formation. Almost complete sequence of the formation is exposed along the Sanaegol Section, 7 km southwest of Hwangjidong in Taebaeg City (Figure 1). In this section, the lower part of the formation is barren of macrofossils. Cephalopod fossils were found in two stratigraphic units, the middle-upper and uppermost parts of the formation (Figure 2).

Lithologic components of the formation consist of bioturbated limestone, well bedded limestone and bioclastic limestone with frequent intercalations of dolomite and dolomitic limestone. Flat pebble conglomerates are included in the lower part of the formation, but they were not observed in the section examined. The boundary between the underlying Maggol and overlying Jigunsan Formations was observed at a small waterfall, about 1.5 km upstream along the valley from Sanaegol village. The lithic facies at this place shows an abrupt change from bioclastic grainstone consisting mostly of oolitic particles to calcareous black shale. Based on the general composition and sedimentary structures such as desiccation cracks, ripple marks, bird's-eye structures, and bioturbation, Paik (1985, 1987, 1988) suggested tidal flats as the depositional environments of the Maggol Formation. Cephalopod fossils were collected mainly from the bioclastic



Figure 1. Index map of fossil locality on the western area of Taebaeg City, Kangweondo.

and bioturbated limestones in the two stratigraphic levels mentioned above, being especially abundant in the uppermost horizon of this formation.

Faunal characteristics and correlation

Based on a relatively limited number of cephalopod specimens, Kobayashi (1966) designated three fossil horizons in the middle and upper parts of the Maggol Formation; *Manchuroceras*, *Polydesmia*, and *Sigmorthoceras* horizons in ascending order (Table 1), and correlated them with upper Canadian, and lower and middle Chazyan (Whiterockian in the present usage) in North America, respectively. Kobayashi (1977) studied Takuhito Shiraki's collection and described four endoceroid species belonging to *Manchuroceras* from the Maggol Formation, without documentation of their exact localities and stratigraphic positions. Since siphuncular remains of *Manchuroceras* were not found in the overlying Jigunsan and Duwibong Formations, Kobayashi (1966) assigned the horizon of the *Manchuroceras* fauna to the middle part of the Maggol Formation.

Table 1. Lithostratigraphic and biostratigraphic division of Ordovician Duwibong type sequence of Joseon Supergroup in Korea (Compiled from Kobayashi, 1966; Kim *et al.*, 1991).

| Formation | Macrofossil zone |
|-----------|------------------------|
| Duwibong | Actinoceroids |
| Jigunsan | Orthoceroids |
| Maggol | <i>Sigmorthoceras</i> |
| | <i>Polydesmia</i> |
| | <i>Manchuroceras</i> |
| | <i>Clarkella</i> |
| Dumugol | <i>Kayseraspis</i> |
| | <i>Protopliomerops</i> |
| | <i>Asaphellus</i> |
| Dongjeom | <i>Pseudokainella</i> |

In this study, 53 cephalopod specimens from seven horizons in the Maggol Formation were collected and analyzed (Figure 2). The following 11 species belonging to 7 genera

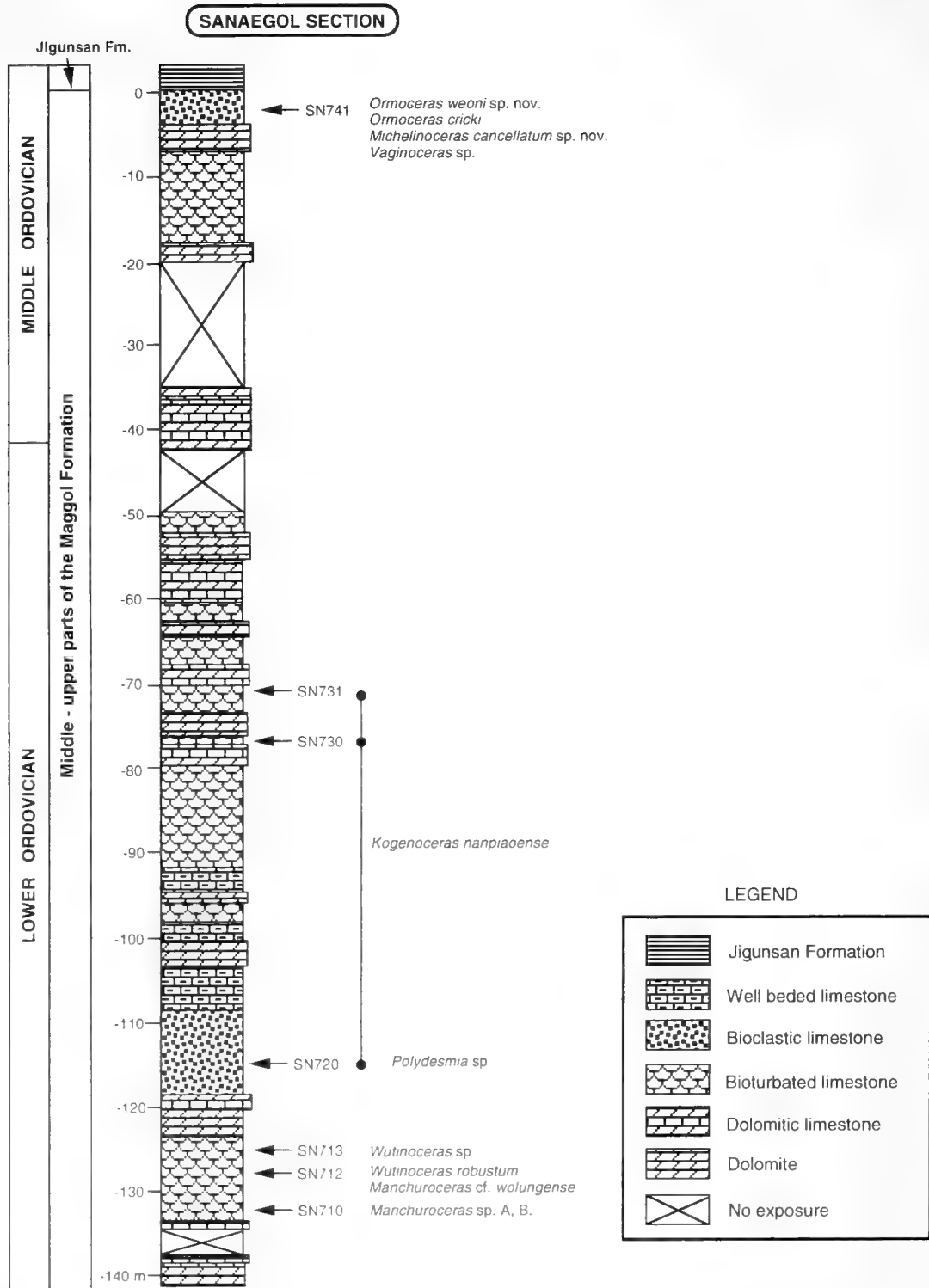


Figure 2. Geologic column of the middle to upper parts of the Maggol Formation at Sanaegol section, showing the cephalopod-bearing horizons. SN stands for the locality name, "Sanaegol".

were recognized: *Ormoceras weoni* sp. nov., *Ormoceras cricki* Kobayashi, 1934, *Michelinoceras cancellatum* sp. nov., *Vaginoceras* sp., *Kogenoceras nanpiaoense* (Kobayashi and Matsumoto, 1942), *Polydesmia* sp. cf. *P. canaliculata* Lorenz, 1906, *Wutinoceras robustum* (Kobayashi and Matsumoto, 1942), *Wutinoceras* sp., *Manchuroceras* sp. cf. *M. wolungense* (Kobayashi, 1931), *Manchuroceras* sp. A, and *Manchuroceras* sp. B.

Of these species, the two *Wutinoceras* species are the first report of the genus in Korea. *Wutinoceras* is widespread in the lower-middle Whiterockian strata of North America (Flower, 1957, 1968, 1976), Australia (Teichert and Glenister, 1953; Flower, 1968; Stait, 1984; Stait and Burrett, 1984), North China (Endo, 1930; Kobayashi and Matsumoto, 1942; Chang, 1965; Zhu and Li, 1996) and Malaysia (Stait and Burrett, 1982). Teichert (1935) and Flower (1968) regarded *Polydesmia* as the oldest and most primitive of the actinoceroids, relying on their thick connecting ring and dendritic

radial canal system. In the Ordovician of China, however, *Polydesmia* does not occur prior to *Wutinoceras* (Chen, 1976; Chen *et al.*, 1980). Therefore, *Wutinoceras* may be the ancestor of the Actinoceratidae, as suggested by Flower (1976).

The three species of *Manchuroceras* from the Maggol Formation listed above are always represented by partial siphuncles and were found in the middle part of the Maggol Formation (Figure 2). The two horizons (SN710 and 712 in Figure 2) yielding these fossils may be equivalent to the *Manchuroceras* horizon of Kobayashi (1966). The genus name *Manchuroceras* was first proposed by Ozaki (1927) without describing its type species, and was subsequently emended and redescribed in detail by Kobayashi (1935). This genus characterizes the Wolungian stage in North China. A total of 28 species assigned to *Manchuroceras* are described from the Ordovician of various regions (Table 2), among which 20 species are known from China, 4 species

Table 2. List of *Manchuroceras* species hitherto described.

| Species | Occurrence | Reference |
|---|---|----------------------------------|
| <i>Manchuroceras</i> nom. nud. Ozaki | Wolungian (Lower Ordovician) limestone of Manchoukou, Manchuria | Ozaki (1927) |
| <i>Manchuroceras wolungense</i> (Kobayashi) | Wolungian (L. Ordovician) limestone of Manchoukou, Manchuria | Kobayashi (1935), Obata (1939) |
| <i>M. endoi</i> Kobayashi | Lower Ordovician Santao Formation, Liaotoug, Manchuria | Kobayashi (1935) cf. Endo (1932) |
| <i>M. ozakii</i> Obata | Daling limestone, Manchuria; Liangjiashan Formation of Hupeh, China | Obata (1939) |
| <i>M. compressa</i> (Kobayashi) | Wolung limestone of Wolung, Manchuria; Liangjiashan Formation of Hupeh, China | Obata (1939) |
| <i>M. platyventrum</i> (Grabau) | Daling limestone, Manchuria; Liangjiashan Formation of Hupeh, China | Obata (1939) |
| <i>M. ishidai</i> Obata | Liangjiashan Formation of Hupeh, China | Obata (1939) |
| <i>M. yenchouchengense</i> Obata | Daling limestone, Manchuria | Obata (1939) |
| <i>M. kobayashii</i> Obata | Liangjiashan Formation of Hupeh; Maggol Formation of Yongyeon-chon, Taebaeg, S. Korea | Obata (1939), Kobayashi (1977) |
| <i>M. katsunumai</i> Obata | Liangjiashan Formation of Hupeh, China | Obata (1939) |
| <i>M. steanei</i> Teichert | L. Ordovician, Adamsfield, Tasmania | Teichert (1947) |
| <i>M. excavatum</i> Teichert | L. Ordovician, Adamsfield, Tasmania | Teichert (1947) |
| <i>M. asiasticum</i> Balashov | Early Middle Ordovician Krivolutsky Formation, Siberia Platform | Balashov (1962) |
| <i>M. sp.</i> | L. Ordovician Lower Jiacun Group of Nyalam, Xiuang, China | Chen (1975) |
| <i>M. qingshuiheense</i> Chen | L. Ordovician Liangchiashan Fm., Qingshuihe, Inner Mongolia | Chen (1976) |
| <i>M. tochuanshanense</i> Chang | Lower Ordovician, upper part of Tochuanshan limestone, Chinghai, N.W. China | Chang (1965) |
| <i>M. lemonei</i> Hook & Flower | Florida Mountains Formation, El Paso, Texas | Hook & Flower (1977) |
| <i>M. cf. platyventrum</i> (Grabau) | Maggol Formation of Gaesan-chon, Taebaeg City, Kangweondo, S. Korea | Kobayashi (1977) |
| <i>M. tenuise</i> Kobayashi | Maggol Formation of Guemdae-chon, Sangjangmyeon, Samcheok-gun, Kangweondo, Korea | Kobayashi (1977) |
| <i>M. hanense</i> Kobayashi | Maggol Formation of Godoo-am, Guraeri, Samgdong, Yeongweol, Kangweondo, S. Koera | Kobayashi (1977) |
| <i>M. ? sp.</i> | Maggol Formation of Godoo-am, Guraeri, Samgdong, Yeongweol, Kangweondo, S. Koera | Kobayashi (1977) |
| <i>M. limatum</i> Xu. | L. Ordovician Honghuayuan Formation of Yichang, Hupeh, Central China | Xu (1981) |
| <i>M. densum</i> Xu | L. Ordovician Honghuayuan Formation of Yichang, Hupeh, Central China | Xu (1981) |
| <i>M. pachymuratum</i> Xu | L. Ordovician Honghuayuan Formation of Yichang, Hupeh, Central China | Xu (1981) |
| <i>M. yangteense</i> Xu | L. Ordovician Honghuayuan Formation of Yichang, Hupeh, Central China | Xu (1981) |
| <i>M. yazipingense</i> Zou | L. Ordovician Liagchishan Formation of Shanxi, North China | Zou (1981) |
| <i>M. minitum</i> Zou | L. Ordovician Liagchishan Formation of Shanxi, North China | Zou (1981) |
| <i>M. pianguanense</i> Zou | L. Ordovician Liagchishan Formation of Shanxi, North China | Zou (1981) |
| <i>M. platyventrum</i> (Grabau) | L. Ordovician Liagchishan Formation of Hebei, North China | Lai <i>et al.</i> (1982) |
| <i>M. nakamense</i> Stait & Burrett | Upper Ibexian Thungsong Formation of Ron Phibum, Southern Thailand | Stait & Burrett (1984) |

from South Korea, 2 species from Tasmania, 1 species from the Siberian Platform, and 1 species from Texas, U.S.A. Most of them, excluding the Russian one, are known to occur in the Lower Ordovician (upper Ibexian). The *Manchuroceras* horizon of the Maggol Formation in Korea is correlated with the Liangchiashan Formation, Hwangho Region and with the Hunghuayuan Formation, Yangtze Region (Chen *et al.*, 1980). The cephalopod fauna including *Manchuroceras nakamense* from the Lower Setul Limestone of Malaysia shows some affinities with that from the Maggol Formation. The OT8 zone of the Karmberg Limestone, Tasmania, proposed by Banks and Burrett (1980) may also be correlated with the Maggol Formation.

The specialized actinoceroid *Polydesmia*, which is characterized by a vertically lamellate structure of the siphuncular filling and high obliquity of the radial canal, is only known from East Asia, including North Korea, Inner Mongolia, South Manchuria and Shandong in China. Kobayashi (1966) designated the *Polydesmia* horizon in the upper part of the Maggol Formation, based on a single specimen of this genus. Unfortunately, he did not illustrate this specimen and it is probably lost. Furthermore, all of the type specimens of the four *Polydesmia* species described by Kobayashi (1940) from China and North Korea are lost. According to Chen *et al.* (1980), *Polydesmia* is typically found in the Lower Ordovician Beianzhuang Formation of Hubei and Shandong in North China, which is conformably underlain by the *Manchuroceras*-bearing Liangchiashan Formation. The occurrence of *Polydesmia* cf. *canaliculata* in the upper part of the Maggol Formation supports the validity of the *Polydesmia* horizon established by Kobayashi (1966). This genus co-occurs with two other genera, *Wutinoceras* and *Manchuroceras* in Korea and China. Since the upper part of the Korean Maggol Formation yields *Polydesmia*, its age is assigned to the early Whiterockian in the North American scale.

Wutinoceras robustum (Kobayashi and Matsumoto, 1942) occurs in the middle part of the Maggol Formation, together with some *Manchuroceras* specimens (Figure 2). The higher horizons (locs. SN730 and 731 in Figure 2) yield the annulated orthoconic cephalopod *Kogenoceras nannipaoense* (Kobayashi and Matsumoto, 1942). These two species have previously been recorded from strata of uncertain age within the Ordovician in Nannipao Coalmine, Nannipao County, Liaoning Province, and were assigned to the Tounfangian in South Manchuria by Kobayashi and Matsumoto (1942). Stait and Burrett (1982) described *W. robustum* from the Lower Setul Limestone of Whiterockian age in the Langkawi Islands, Malaysia. Subsequently, Stait *et al.* (1987) described *Kogenoceras nannipaoense* from a slightly higher horizon than the *W. robustum*-bearing strata in the same area and assigned it a Whiterockian age. These lines of evidence suggest that the cephalopod fauna of the Maggol Formation has strong affinities to the Southeast Asian and North Chinese faunas of equivalent age.

Four species belonging to 3 genera were identified among many small-sized cephalopod specimens recovered from the horizon just below the boundary of the Maggol and Jigunsan Formations (loc. SN741 in Figure 1). Of these species, *Ormoceras weoni* sp. nov. and *O. cricki* occur most abundant-

ly, making up more than 90 per cent of the cephalopod assemblage. The latter species is common in the Duwibong Formation, the uppermost Ordovician formation in Korea (Kobayashi, 1934), indicating that this species has a long range from the Maggol Formation to the Duwibong Formation. This species possibly represents the oldest type of the ormocerids in the upper Jigunsan and Duwibong Formations.

Systematic paleontology

The terminology and measurements of various shell morphological characters used in this paper are shown in Figure 3.

Subclass Endoceratoidea Teichert, 1933

Order Endocerida Teichert, 1933

Family Manchuroceratidae Kobayashi, 1935

Genus *Manchuroceras* Ozaki, 1927 emend. Kobayashi, 1935

Type species: *Piloceras wolungense* Kobayashi, 1931

Manchuroceras sp. cf. *M. wolungense* (Kobayashi, 1931)

Figures 4-1a, b; 7-5a, b

Material.—Isolated partial siphuncle, KPE20073 from loc. SN712.

Description.—Partial siphuncle with apical end, 71.2 mm in length; its dorsal side somewhat weathered and apical portion distorted by local joint and calcite vein; apex bluntly pointed; dorsoventral and lateral diameters nearly equal at a distance of 49.7 mm from apex, i.e., circular in cross section, 30.5 mm in diameter; inner side of siphuncle lined with crystalline calcite, recrystallized endosiphosheaths, this lining thinnest on dorsal side, becoming thicker laterally, ventral side of siphuncle strengthened by additional deposits, forming endosiphowedge, 12.4 mm thick at a distance of 49.7 mm from apex; endosiphococone rapidly expanding, its apical angle approximately 45 degrees, its apex continuing into endosiphotube, in which endosiphuncular segments are detected.

Remarks.—This species appears to be closely allied to *Manchuroceras wolungense* (Kobayashi) from the Wolung Limestone of South Manchuria (Kobayashi, 1931 p. 170, pl. 17, figs. 2, 3a, b, 6; pl. 18, figs. 2a, b; pl. 19, fig. 1) in having a circular cross section of the siphuncle and well developed endosiphowedge. Specific identification requires additional better preserved specimens.

Occurrence.—Known from the middle part of the Maggol Formation of Sanaegol, Taebaeg City, Kangweondo, South Korea.

Manchuroceras sp. A

Figures 4-2a, b; 7-1a—c

Material.—Isolated partial siphuncle, KPE20256 from loc. SN710.

Description.—Internal mould of siphuncle, 77.7 mm long; straight, with its diameter expanding twice as rapidly laterally

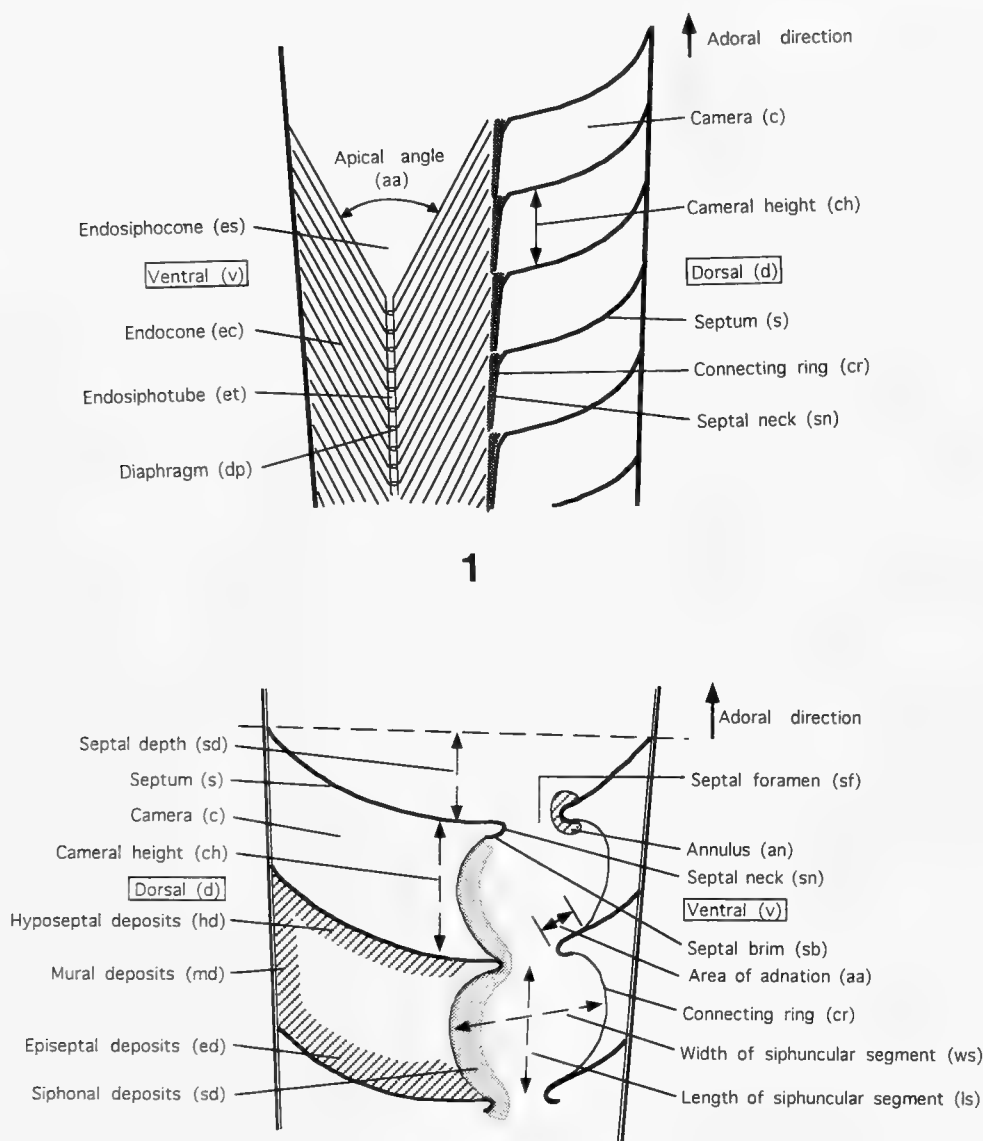


Figure 3. Terminology and measurements of internal shell structures of idealized endoceroid (1) and actinoceroid (2) cephalopods used in this paper. Abbreviations of various shell characters are written in parentheses. Compiled and modified from Teichert *et al.* (1964), Aronoff (1979), and Zhu and Li (1996).

as dorsoventrally; its cross section circular in juvenile stage, but becomes elliptically depressed with growth, ratio of dorsoventral to lateral diameters of siphuncle at adoral end being 3:4; endosiphuncular deposits nearly uniform in thickness, not forming endosiphonwedge, endocones recrystallized; endosiphococone slender, deep, rapidly expanding with apical angle of 25 degrees, its apex acutely pointed and situated at endosiphuncular center, continuing into endosiphotube which pierces apex; outside of siphuncle appears to be smooth.

Remarks.—This species is allied to *Manchuroceras tenuise* Kobayashi from Guemdae-chon, Taebaeg City, Kangweondo (Kobayashi, 1977) in the small apical angle of the endosi-

phococone and ovate cross section, but is distinguished by evenly thickened endosiphuncular linings. *Manchuroceras yenchouchengense* Obata from the Daling Limestone of Liaoning, South Manchuria (Obata, 1939, p. 103, pl. 7, figs. 4, 6; pl. 8, fig. 2; pl. 10, fig. 6) may be related to this species in the elliptical cross section, but its blunt endosiphococone and greater dorsoventral diameter serve to distinguish this species from *M. yenchouchengense*. This comparison indicates that the present species belongs to *Manchuroceras*, but well preserved additional specimens are needed for species-level assignment.

Occurrence.—Known only from the middle part of the Maggol Formation in Sanaegol.

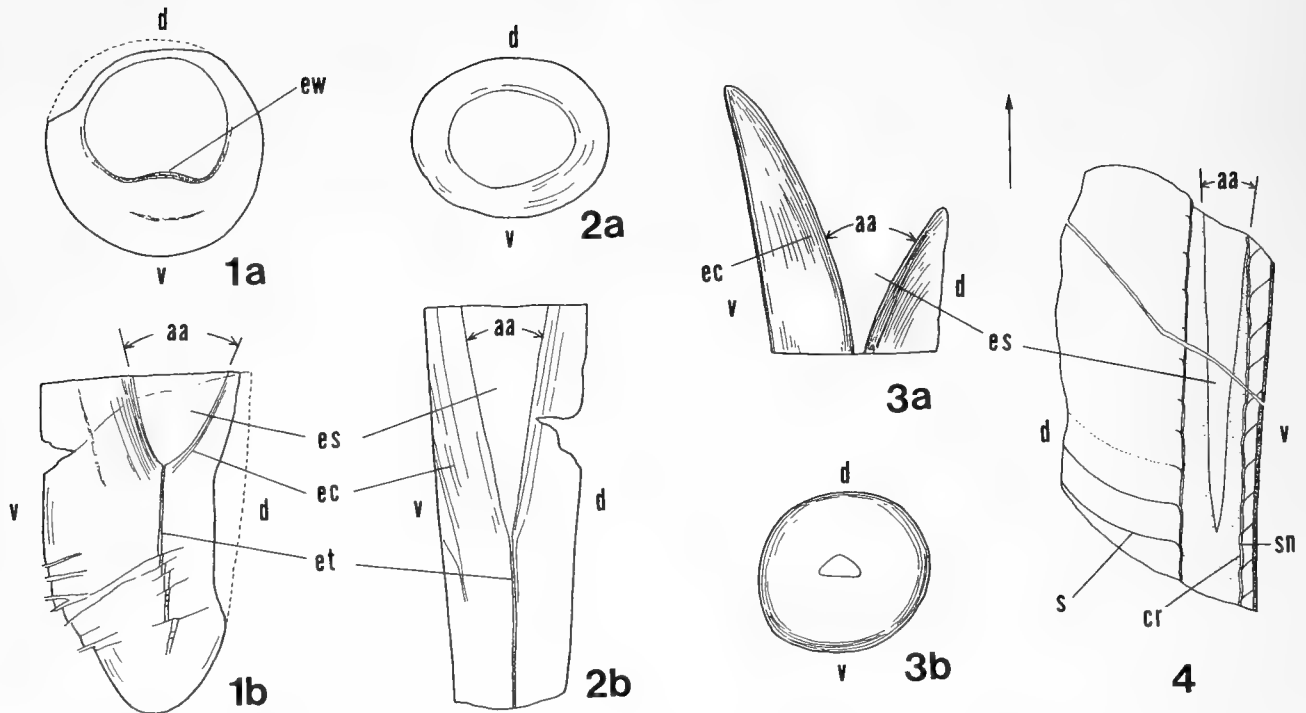


Figure 4. Diagrammatic drawings of endoceroid cephalopods described herein. **1a, b.** *Manchuroceras* sp. cf. *M. wolungense* (KPE20073), $\times 0.9$, 1a: cross section at the adoral end, 1b: longitudinal section. **2a, b.** *Manchuroceras* sp. A (KPE20256), $\times 1$, 2a: cross section at the adoral end, 2b: longitudinal section, **3a, b.** *Manchuroceras* sp. B (KPE20065), $\times 0.9$, 3a: longitudinal section, 3b: cross section at the adapical end, **4.** *Vaginoceras* sp. (KPE20230), $\times 1.4$. The arrow indicates the adoral direction for 1b, 2b, 3a, and 4. For abbreviations see Figure 3, except for ew: endosiphowedge.

Manchuroceras sp. B

Figures 4-3a, b; 7-4a, b

Manchuroceras sp. indet. Kobayashi, 1977, p. 24, pl. 3, figs. 3a, b.

Material.—Partial siphuncle, KPE20065 from loc. SN710.

Description.—Imperfect siphuncle; slowly expanding, with apical angle 13 degrees; adapical end circular in cross section but endosiphococone triangular, its tip somewhat rounded, more flattened ventrally than dorsally, its basal length and height 5 mm and 2.5 mm, respectively; apical angle of endosiphococone about 65 degrees, but abruptly decreasing toward adapical end at broadly curving point of endosiphocline, attaining 15 degrees; endocone asymmetrical, rapidly extending anteriorly and more thickened on ventral side than on dorsal side, numerous lamelliform endocones well developed; no cameral portion detected.

Remarks.—This species is allied to *Manchuroceras tenuise* Kobayashi from Guemdae-chon, Sangjangmyeon, Samcheok, Kangweondo, Korea (Kobayashi, 1977, p. 23, pl. 4, figs. 2a, b) in its triangular endosiphococone in cross section, but differs by its centrally located and more slowly expanding endosiphococone. This species is distinguished from *Manchuroceras* sp. A described above, in the much more rapidly expanding endosiphococone.

Meanwhile, the apical angle of the endosiphococone and

thickness of endocone in this species are similar to those in the specimen of *Manchuroceras* ? sp. indet. described by Kobayashi (1977) from Godoo-am, Guraeri, Sangdong, Yeongweol. However, incomplete preservation of the present specimen precludes exact specific assignment.

Occurrence.—Known only from the middle part of the Maggol Formation in Sanaegol.

Family Endoceratidae Hyatt, 1883

Genus *Vaginoceras* Hyatt, 1883

Type species: *Endoceras multitubulatum* Hall, 1847

Vaginoceras sp.

Figures 4-4; 7-2a, b

Material.—Partial phragmocone, KPE20230 from loc. SN741.

Description.—Partial phragmocone, 36 mm in length, medium-sized orthocone containing endosiphococone; conch wall 0.6 mm thick on ventral side; slowly expanding; somewhat laterally compressed, ratio of dorsoventral to lateral diameter about 1.4:1; siphuncle submarginal in position, 1.5 mm distant from ventral margin, nearly circular in cross section, broad, its diameter a little less than one-third of dorsoventral conch diameter; septa on dorsal portion mostly obliterated during fossilization, but two preserved septa at

basal part having septal depth one and a half times the cameral height, while septa on ventral side are comparatively well preserved, attached to ventral wall at an angle of 45 degrees; septal necks holochoanitic, extending just to preceding ones; connecting rings about three times thicker than septal neck, embracing inside of septal necks; cameral height 2.5 mm, six camerae distributed in a length corresponding to dorsoventral conch diameter at adoral end; no cameral deposits observed; siphonal deposits well developed, dorsally more extended in longitudinal section, long and slender endosiphococone bounded by last endocone having wedge-shaped section and its apical angle about 15 degrees; shell surface smooth.

Remarks.—The presence of a thick connecting ring and acute endosiphococone indicates that this species belongs to *Vaginoceras*. Unfortunately, incomplete preservation of the specimen examined precludes species-level assignment.

In the long endosiphococone and ectosiphuncular morphology, this species can be allied to *Vaginoceras endocylindricum* Yü from the beds just below the red limestone near Tawushu, north of the western end of Peiyangshan, Chungyanghsien (Yü, 1930, p. 33, pl. 2, figs. 5a–c; pl. 3, figs. 2a–d, 3a, b), but the former is distinguished from the latter by more closely spaced septa and more compressed conch.

Occurrence.—Known only from the uppermost part of the Maggol Formation in Sanaegol.

Order Orthoceratida Kuhn, 1940
Superfamily Orthocerataceae M'Coy, 1844
Family Orthoceratidae M'Coy, 1844
Subfamily Michelinoceratinae Flower, 1945
Genus ***Michelinoceras*** Foerste, 1932

Type species: *Orthoceras michelini* Barrande, 1866

***Michelinoceras cancellatum* sp. nov.**

Figures 5-1; 7-7, 8a–c

Type material.—Holotype, KPE20254 and paratype, KPE20255 both from loc. SN741.

Diagnosis.—Longiconic orthocone with circular cross section; siphuncle central; septal spacing wide; camerae with well developed mural-episeptal deposits; surface ornamented with transverse lines and very fine longitudinal lirae, forming cancellate markings.

Description.—Holotype, KPE20254 (Figures 5-1 and 7-8a–c) represented by a partial phragmocone of juvenile conch; very slender, longiconic orthocone, 21.4 mm in length, consisting of 8 camerae; circular in cross section; very slowly expanding at a rate of 1 mm in 15 mm; siphuncle central in position, tubular, parallel to shell wall, narrow, about 1 mm in diameter, corresponding to one-sixth of conch diameter; septa gently concave adorally; its depth one-third of cameral height, septal necks short, orthochoanitic; connecting rings thin; septa broadly spaced, averaging 2 mm distant between them, 2.5 camerae occurring in a length equal to conch diameter of 6.1 mm; camerae with L-shaped mural-episeptal deposits, remaining space filled with öoid particles and inorganic matrix; siphuncle filled with some

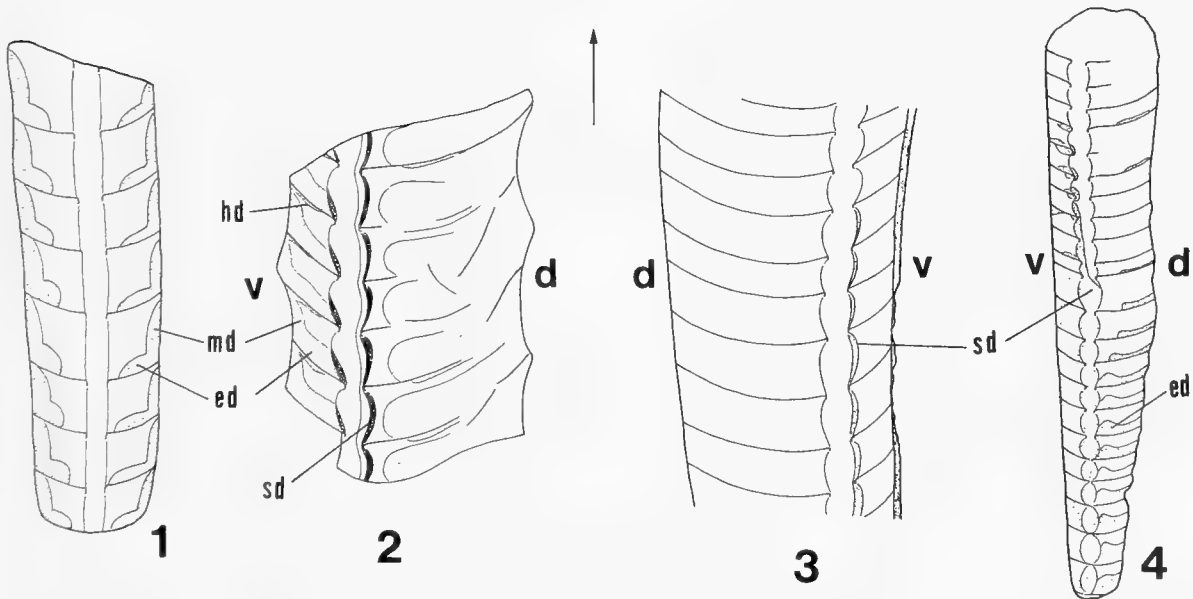


Figure 5. Diagrammatic drawings of median dorsoventral section of orthocerid (1-2) and actinocerid (3-4) cephalopods described herein. 1. *Michelinoceras cancellatum* sp. nov. (holotype; KPE20254), $\times 1.5$, 2. *Kogenoceras nampiaoense* (KPE20208), $\times 2$, 3. *Ormoceras weoni* sp. nov. (holotype; KPE20260), $\times 2$, 4. *Ormoceras cricki* (KPE20232), $\times 2.5$. For abbreviations see Figure 3.

oids and matrix; surface ornamented with transverse growth lines and longitudinal lirae, forming cancellate network, spaces between growth lines and between lirae 0.16 mm and 0.07 mm respectively

Paratype, KPE20255 (Figure 7-7), a partial phragmocone consisting of 9 camerae, 33.2 mm long; probably belongs to adolescent stage in view of higher camera and broader conch than those of holotype; siphuncle central, cylindrical, narrow; septal distance increasing from 3 mm to 3.5 mm during the stage observed; camera with mural-episeptal deposits.

Remarks.—In the surface ornament pattern, this species resembles *Michelinoceras reticulatum* (Kobayashi) from the Jigunsan Formation of Homyeong (Kobayashi, 1934, p. 406, pl. 16, figs. 3-5). In the former species, however, are weaker and thinner longitudinal lirae than transverse growth lines, whereas in the latter species transverse lines are more crowded than longitudinal ones. In addition, the siphuncle in the present species is central in position, not submarginal as in *M. reticulatum*.

This species is similar to *Michelinoceras shangliense* Qi from the Middle Ordovician Datianba Formation of Anhui, China (Qi, 1980, p. 251, pl. 4, fig. 1) in the expansion rate of conch and septal spacing, but the former is distinguished from the latter by its peculiar latticed ornamentation and central siphuncle. This species is also allied to *Michelinoceras paraelongatum* Chang from the Middle Or-

dovician of Gansu, North China (Chang, 1962, p. 517, pl. 1, figs. 5a-c) in its small-sized conch with circular cross section, but the former has more narrowly spaced septa and broader siphuncle than the latter. In its surface markings, *Michelinoceras guichiense* Ying from the Middle Ordovician Datianba Formation of Guichi, Anhui, China (Ying, 1989, p. 630, pl. 3, figs. 5, 6) exhibits an affinity to the present species, but longitudinal lirae occurring in the present species are absent in *M. guichiense*.

Occurrence.—Known only from the uppermost part of the Maggol Formation in Sanaegol.

Superfamily Pseudorthocerataceae Flower and Caster, 1935

Family Stereoplasmoceratidae Kobayashi, 1934

Genus ***Kogenoceras*** Shimizu and Obata, 1936

Type species: *Tofangoceras huroniforme* Kobayashi, 1927

Kogenoceras nanpiaoense

(Kobayashi and Matsumoto, 1942)

Figures 5-2; 7-3, 6, 9a, b

Tofangoceras nanpiaoensis Kobayashi and Matsumoto, 1942, p.

313, pl. 31, figs. 10-12; Chao *et al.*, 1965, p. 96, pl. 22, fig. 11.

Kogenoceras nanpiaoense (Kobayashi and Matsumoto). Chen *et al.*, 1980, p. 177, pl. 3, fig. 18; Text-fig. 10; Lai *et al.*, 1982, pl. 6, figs. 12, 13; Stait, Wyatt and Burrett, 1987, p. 385, figs. 6-2-4.

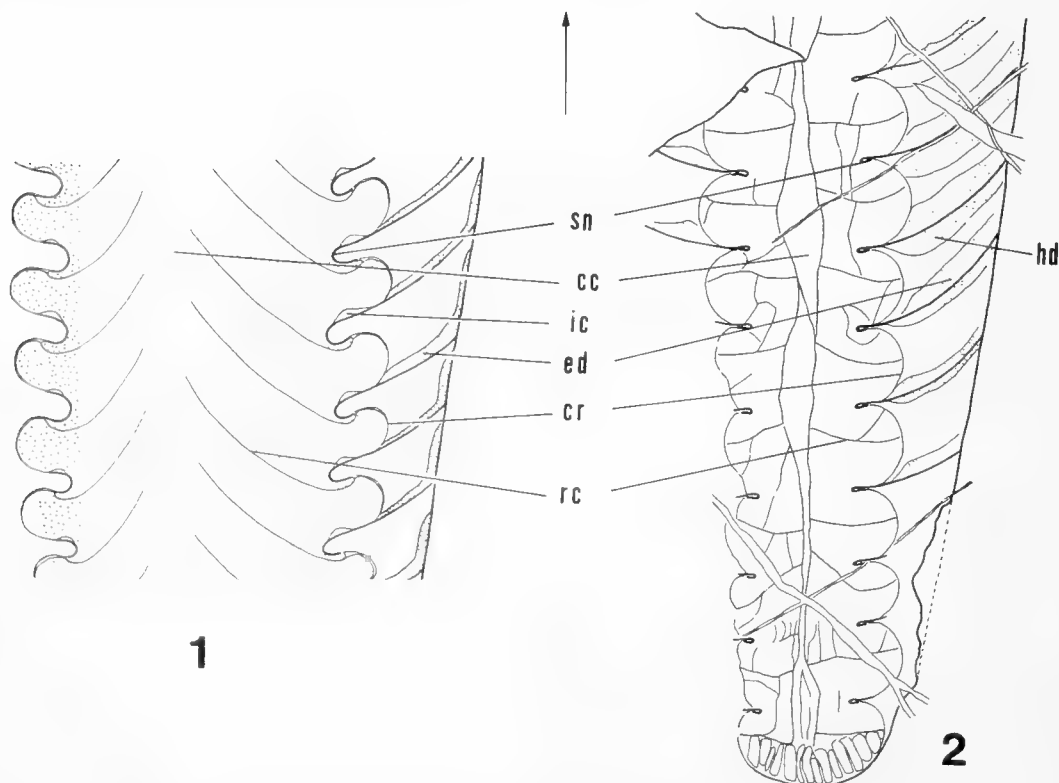


Figure 6. Diagrammatic drawings of actinoceroid cephalopods described herein. 1. *Polydesmia* sp. cf. *P. canaliculata* (KPE20323), $\times 1$. 2. *Wutinoceras robustum* (KPE20206), $\times 1$. For abbreviations see Figure 3, except for ic: interseptal cavity, cc: central canal, rc: ardiol canal.

Material.—Six partial phragmocones from the upper part of the Maggol Formation at localities, SN720 (KPE20282, 20283 and 20327), SN730 (KPE20209), and SN731 (KPE20208 and 20210).

Diagnosis.—Annulated cyrtochoanitic orthocone; camerae with episeptal and hyposeptal deposits; siphuncle with dorsally intermittent and ventrally connected parietal deposits.

Description.—Medium-sized annulated longiconic orthocone with eccentric siphuncle.

KPE20208 (Figures 5-2, 7-9a, b), a fragmentary phragmocone with 6 siphuncular segments, 21 mm long, very slowly enlarging, circular in cross section; siphuncle eccentric, midway between center and venter, narrow, occupying a little more than one-sixth of dorsoventral conch diameter; siphuncular segments *Huronio*-like in shape, greatly expanding in upper third, 2.8 mm in length and 2.3 mm in maximum diameter, contracting to 1.2 mm at septal foramen; septa gently concave adorally, partly crushed on dorsal side, septal depth equal to half or more of the cameral height; septal neck cyrtochoanitic, short, 0.3 mm in length; cameral height low, about 2.8 mm at upper part, 5 camerae in a length corresponding to the dorsoventral conch diameter on the crest of annuli; connecting rings thin, not adnate to the septa; camera filled with both episeptal and hyposeptal deposits; siphuncle deposits with parietal deposits consisting of longitudinal thin lamellae, dorsally occurring successively whereas ventrally intermittent; surface ornamented with strong annulations at intervals of 7.3 mm wide, corresponding to 2.5 camerae, its height from the base of the interspace about 0.8 mm.

KPE20209 (Figure 7-3), 49 mm in length, its adapical portion not preserved; conch nearly circular in cross section; siphuncle close to venter, narrow, its width one-eighth of dorsoventral conch diameter; siphuncular segments somewhat expanded between septal foramina at a point about one fourth from its anterior end, ratio of width to length 0.8; septa crowded, septal depth attaining one and a half times cameral height; camerae with both epi- and hyposeptal deposits, but siphuncular deposits not distinctly detected; surface ornamented with broadly rounded annulations at intervals of 6 mm.

Remarks.—Kobayashi and Matsumoto (1942) proposed *Tofangoceras nanpiaoensis* from the Tofangian, Nanpiao Coalmine, based on the type specimen, UMUT PM1903 which are characterized by well-developed endosiphuncular deposits and submarginal siphuncle with the *Huronio*-like siphuncular segments. However, Chen *et al.* (1980) and Stait *et al.* (1987) attributed the generic position of this species to *Kogenoceras* of Shimizu and Obata (1936) because of the characteristic features of *Kogenoceras* such as cyrtochoanitic annulated orthoceracone, circular cross section, and narrow eccentric siphuncle, with *Huronio*-like segments. The enlarged photo of the siphuncle of *K. nanpiaoense* from the Lower Ordovician Lower Setul Limestone of the Langkawi Islands, Malaysia (Stait *et al.*, 1987, p. 386, fig. 6-4) shows cyrtochoanitic septal necks, though these authors mistakenly described the septal neck type as orthochoanitic.

This species is similar to *Kogenoceras huroniforme*

(Kobayashi) from the Duwibong Formation of Hwarari, Kangweondo, Korea (Kobayashi, 1934, p. 435, pl. 27, figs. 9-11, 14) in the *Huronio*-like siphuncular segments and eccentric siphuncle, but is easily distinguished by the presence of the parietal deposits along the siphuncular wall.

Occurrence.—In addition to the present material, specimens assigned to this species are known from the Lower Ordovician of Nanpiao Coalmine, Nanpiao County, Liaoning Province, South Manchuria (Kobayashi and Matsumoto, 1942; Lai *et al.*, 1982), Beianzhuang Formation of Shandong, North China (Chen *et al.*, 1980) and the Lower Setul Limestone on the east coast of Pulau Langgun, Langkawi Islands, Malaysia (Stait *et al.*, 1987).

Order Actinocerida Teichert, 1933

Family Ormoceratidae Saemann, 1853

Genus *Ormoceras* Stokes, 1840

Type species: *Ormoceras bayfieldi* Stokes, 1840

Ormoceras cricki Kobayashi, 1934

Figures 5-4; 8-1-8

Ormoceras cricki Kobayashi, 1934, p. 444, pl. 23, fig. 7; pl. 25, fig. 7.

Ormoceras sp. B., Chang, 1959, p. 266, pl. 5, fig. 5.

Material.—15 specimens, KPE20231-20245 from loc. SN741, among which 14 are partial phragmocones and one (KPE20231) is a well-preserved, almost complete adult conch.

Diagnosis.—Conch cross section elliptical in juvenile stage, but becomes subcircular in adult stage; eccentric siphuncle with globular segments; camera with episeptal deposits forming a pointed ridge just in front of connecting ring; hyposeptal deposits absent; siphuncle filled with parietal deposits along the inside of connecting ring.

Description.—Small to medium-sized cyrtochoanitic longiconic orthoceracone; smooth shell, no sculpture discernible; conch cross section strongly depressed, elliptical in juvenile stage, but becoming subcircular with growth, adult body chamber nearly circular in cross section; its diameter moderately expanding at a rate of 1 mm per 8 mm in lateral and dorsoventral lengths; siphuncle eccentric, close to venter, located at about 2/3 of conch diameter from dorsal margin, narrow, its diameter a third of dorsoventral conch diameter in juvenile stage, but becoming smaller, being one-fifth of the corresponding diameter in the adolescent shell because of nearly uniform expansion rate of siphuncle; siphuncular segments globular, as long as broad; septa gently concave adorally, septal depth as wide as a half of cameral height; septal necks cyrtochoanitic, abruptly recurved, adnate for a short distance to adapical part of connecting ring, but just meeting the adoral end of connecting ring; septal brim very short; suture directly transverse, but slightly sloping from dorsal to ventral side; camerae low, increasing from 1.1 mm to 1.5 mm during ontogeny, four camerae occurring in a length equal to dorsoventral conch diameter of 6.5 mm in KPE20232 (Figures 5-4 and 8-2b); camera with well-developed mural-episeptal deposits, in which mural deposits

vestigial dorsally but more concentrated ventrally.

The degree of development of cameral deposits changes during ontogeny (see Figure 5-4); In juvenile stage, dorsal episepal deposits becoming thicker toward nummuli, forming a pointed ridge just in front of connecting ring and abruptly thinning out to a saucer-like shape, the apex of pointed ridge rather acute and gradually shifting to the shell wall adorally whereas it is difficult to recognize on the ventral side due to secondary recrystallization. In adolescent stage, episepal deposits shortened dorsally, not swollen and mural-episepal deposits still thicker ventrally. In adult stage cameral deposits seldom present.

Siphuncle filled with biogenic deposits in both juvenile and adolescent stages. The deposits more heavily developed ventrally than dorsally in adult stage, subsequently appearing to be annulosiphonate deposits ventrally.

Remarks.—This species resembles *Ormoceras woodwardsi* Kobayashi from the Jigunsan Formation of Homyeong, Jeongseon (Kobayashi, 1934, p. 445, pl. 31, fig. 5) in the globular siphuncular segments and submarginal siphuncle, but is distinguished by the absence of episepal deposits. It is similar to *Ormoceras harioi* (Kobayashi) from the Tofango Limestone of Tofango, South Manchuria (Kobayashi, 1927, p. 196, pl. 22, fig. 12; pl. 21, fig. 9) in having episepal deposits, but differs from the latter in the broader siphuncle in proportion to conch diameter and the more rapidly expanding conch.

In the saucer-like shape of episepal deposits, *Parormoceras nanum* (Grabau) from the Tofango Limestone of South Manchuria (Kobayashi, 1927, p. 195, pl. 20, fig. 11; pl. 21, fig. 8; pl. 22, fig. 5) is closely related to this species, but the former is distinguished from this latter by the presence of such characters as *Huronella*-like siphuncular segments, more rapidly expanding conch and more closely spaced septa.

Occurrence.—In addition to the uppermost horizon of the Maggol Formation of Sanaegol described herein, this taxon is known from the Duwibong Formation of Hwajeolchi, Jungdong-myeon, Yeongweol area, and of Homyeong, Dongmyeon, Jeongseon area and Gaesandong, Taebaeg City, Kangweondo (Kobayashi, 1934).

Ormoceras weoni sp. nov.

Figures 5-3; 8-9-12; 9-1-3

Types.—Holotype, KPE20260, an incomplete phragmocone with an adjacent part of body chamber; 7 paratypes, KPE20261-20267, all from loc. SN741.

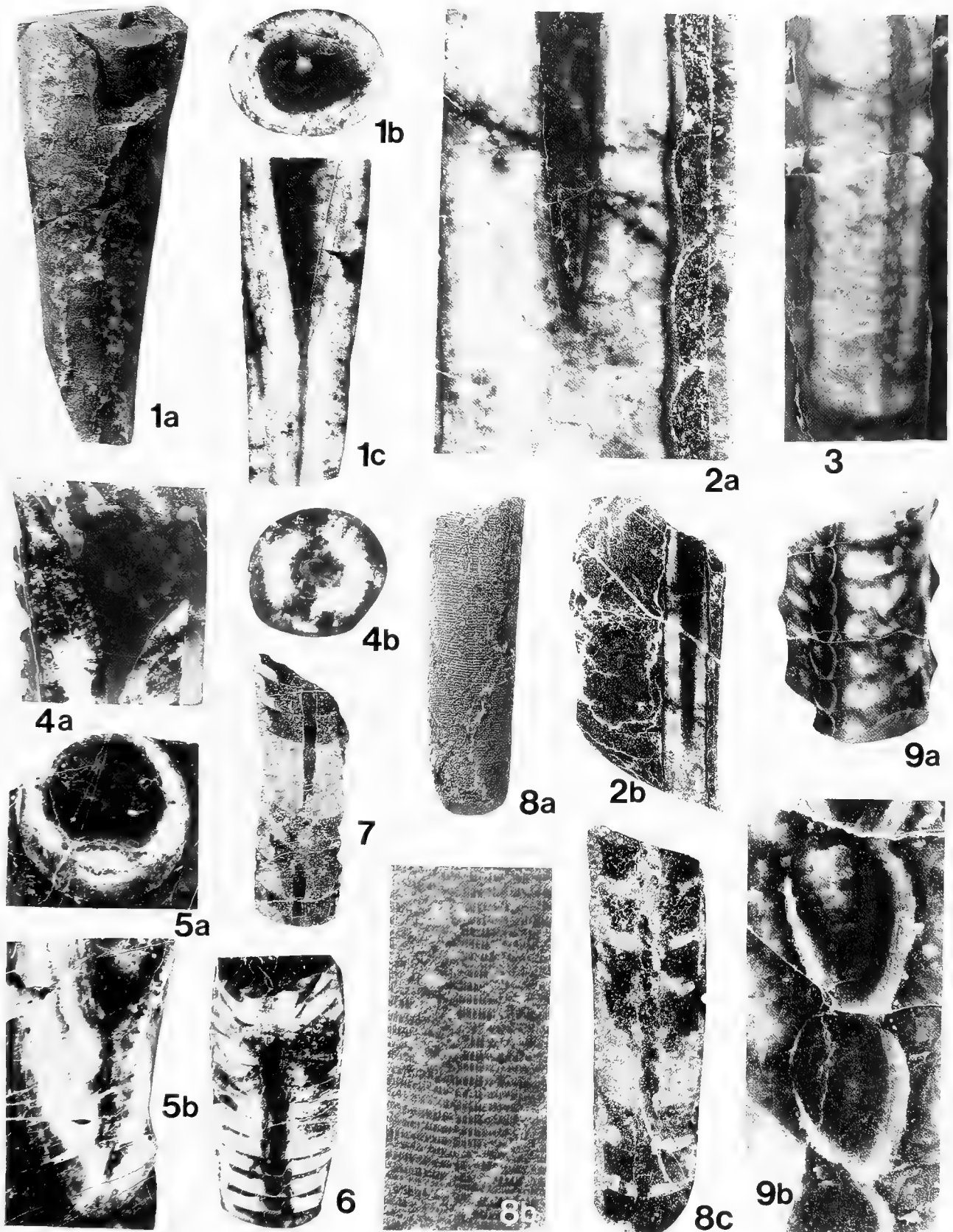
Material.—In addition to the above type specimens, seven specimens (KPE20268-20274) belong to this species. Of these, six (KPE20268-20273) were collected from the type locality, while one (KPE20330) came from the equivalent horizon of the Maggol Formation at Sesong.

Etymology.—The specific name is dedicated to Dal-Gi Weon, who collected many Paleozoic fossils from Kangweondo region and kindly provided some specimens to the author.

Diagnosis.—Longiconic or slightly curved orthocone; conch subcircular, ovately elliptical in cross section; body chamber long; siphuncle submarginal; siphuncular segments somewhat expanded; no cameral deposits detected.

Description.—Medium-sized longiconic or slightly curved orthocone; conch diameter moderately expanding at a rate of 1 mm per 6.5 mm in conch height of the holotype (Figures 8-9a-d); body chamber long; ovately elliptical in cross section, ratio between dorsoventral and lateral diameters at the apical end 4:5 in one of the paratypes (KPE20262; Figure 9-1b); siphuncle submarginal, narrow, occupying about one-eighth of dorsoventral conch diameter; siphuncular segments nummuloidal, more or less expanded, 1.5 mm long and 1.1 mm in maximum diameter in the upper third of the height within camerae, contracting to 0.6 mm at the septal foramen in the holotype; septa gently concave adorally, septal depth ranging from one to one and a half of cameral height, septal necks cyrtchoanitic, very short, just meeting the adoral end of connecting ring; septal spacing narrow, 7 to 8 camerae within the corresponding length of dorsoventral conch diameter; suture directly transverse in two steinkern specimens, KPE20264 (Figure 8-12) and KPE20265 (Figure 8-11); no cameral deposits detected; siphuncle filled with inorganic matrix, but in the holotype and one of the paratypes (KPE20262; Figure 5-1d), endosiphuncular deposits line siphonal surface of venter; surface smooth.

Figure 7. 1a-c. *Manchuroceras* sp. A. partial siphuncle, KPE20256 from SN710, $\times 1$, 1a: ventral view, 1b: cross section at the adoral portion, venter down, 1c: longitudinal section, venter on left, showing endocones and endosiphuncle. **2a, b.** *Vaginoceras* sp. partial phragmocone, KPE20230 from SN741, 2a: detail of siphuncle and ventral camerae, showing very slender endosiphuncle, $\times 5$, 2b: longitudinal section, venter on right, $\times 1.5$. **3, 6, 9a, b.** *Kogenoceras naniplaoense* (Kobayashi and Matsumoto, 1942). 3. Partial phragmocone, KPE20209 from SN730, longitudinal section, venter on right, $\times 1.5$, 6: Partial phragmocone, KPE20282 from SN720, longitudinal section in lateral direction, $\times 1$, 9a, b: Partial phragmocone, KPE20208 from SN731, 9a: longitudinal section, venter on left, $\times 2$, 9b: enlarged view of siphuncular structure, showing parietal deposits and moderately expanded siphuncular segments, $\times 7$. **4a, b.** *Manchuroceras* sp. B. partial siphuncle, KPE20065 from SN710, $\times 1$, 4a: longitudinal section, venter on left, showing more prolonged ventral endocone adorally, 4b: cross section at the adapical end, venter down, showing triangular endosiphuncle with flattened ventral side. **5a, b.** *Manchuroceras* sp. cf. *M. wolungense* (Kobayashi, 1931), partial siphuncle, KPE20073 from SN712, $\times 1$, 5a: cross section at the adoral end, venter down, showing circular outline and endosiphon wedge, 5b: longitudinal section, venter on left, showing the blunt apical end and endosiphon tube. **7, 8a c.** *Michelinoceras cancellatum* sp. nov. 7. Partial phragmocone, paratype, KPE20255 from SN741, longitudinal section, acetate peel, $\times 1.5$, 8a c. Partial phragmocone, holotype, KPE20254 from SN741, 8a: side view, $\times 2.5$, 8b: details of surface ornamentation, showing cancellate ornaments, $\times 12$, 8c: longitudinal section, acetate peel, showing well developed mural-episepal deposits, $\times 3.5$.



Remarks.—This present species closely resembles *Ormoceras yokoyamai* (Kobayashi) from the Jigunsan Formation of Maggol and Homyeong (Kobayashi, 1934, p. 439, pl. 27, figs. 1–6; pl. 28, fig. 2) in the narrow, submarginal siphuncle with somewhat expanded segments, but differs from the latter by the presence of endosiphuncular linings and the lack of ventral flattening in cross section.

Ormoceras cricki Kobayashi from the Duwibong Formation of Homyeong and Gaesanchon (Kobayashi, 1934, p. 444, pl. 23, fig. 7; pl. 25, fig. 7) and from the uppermost bed of the Maggol Formation at Sanaegol (see Figures 8–1—8 in this paper) is allied to this present species in having closely spaced septa and ectosiphuncular morphology. The former, however, can be distinguished from the latter by the presence of episepal deposits, more depressed conch, and much smaller siphuncular diameter in relation to conch diameter.

Occurrence.—Known only from the uppermost part of the Maggol Formation in Sanaegol.

Family Polydesmiidae Kobayashi, 1940

Genus *Polydesmia* Lorenz, 1906

Type species: *Polydesmia canaliculata* Lorenz, 1906

Polydesmia sp. cf. *P. canaliculata* Lorenz, 1906

Figures 6–1; 9–4a, b

Material.—Fragmentary phragmocone, KPE20323 from loc. SN720.

Description.—Longiconic orthocone, 97 mm long, naturally weathered to the level of siphuncle; outline of cross section unknown; siphuncle large, slightly eccentric, conch diameter slowly expanding at a rate of 1 mm per 8 mm in conch height at the adapical portion; siphuncular segments very wide and comparatively low; septal necks cyrtochaonic, evenly curved and long, equalling about one-third of cameral height, represented by a septal loop which corresponds to two-thirds of a circle; septal brims broad, moderately separated from septum; connecting rings thick, expanded largely into camerae, its posterior part forming a triangular elevation toward adoral side (ic in Figure 6–1), which was called “inter-septal cavity” by Kobayashi (1940, p. 36); posterior area of adnation very broad; septa moderately concave adorally, septal depth equivalent to one and a half times or less of cameral height; camerae low, 3.2 mm high; endosiphun-

cular canal system of dendritic type, central canal narrow, off-center, radial canal steeply oblique, extending adapically through about 2 siphuncular segments before entering perispatium, its terminating point located at the tip of septal brim; annuli projected toward antero-inner side, horn-shaped in longitudinal section, internal lamellate structure obscure owing to recrystallization; camerae with mural-episepal deposits.

Remarks.—This species is most closely allied to *Polydesmia canaliculata* Lorenz from south of Chiang-chiawan, Liaoyang-hsien, Manchoukuo, North China (Kobayashi, 1940, p. 34, pl. 3, figs. 1–3 and pl. 4, figs. 17–19) in having the strongly oblique radial canal and triangular interseptal cavity, but incomplete preservation of the present specimen without conch outline and siphuncular position precludes exact species-level assignment.

Occurrence.—Known only from the upper part of the Maggol Formation of Sanaegol.

Family Wutinoceratidae Shimizu and Obata, 1936 emend. Flower, 1968

Genus *Wutinoceras* Shimizu and Obata, 1936 emend. Flower, 1957

Type species: *Nybyoceras foerstei* Endo, 1930

Wutinoceras robustum (Kobayashi and Matsumoto, 1942)

Figures 6–2; 10–1, 2

Jeholoceras robustum Kobayashi and Matsumoto, 1942, p. 315, pl. 30, figs. 1–5; pl. 31, fig. 6.

Armenoceras robustum (Kobayashi and Matsumoto). Chao et al., 1965, p. 70, pl. 17, figs. 7–9.

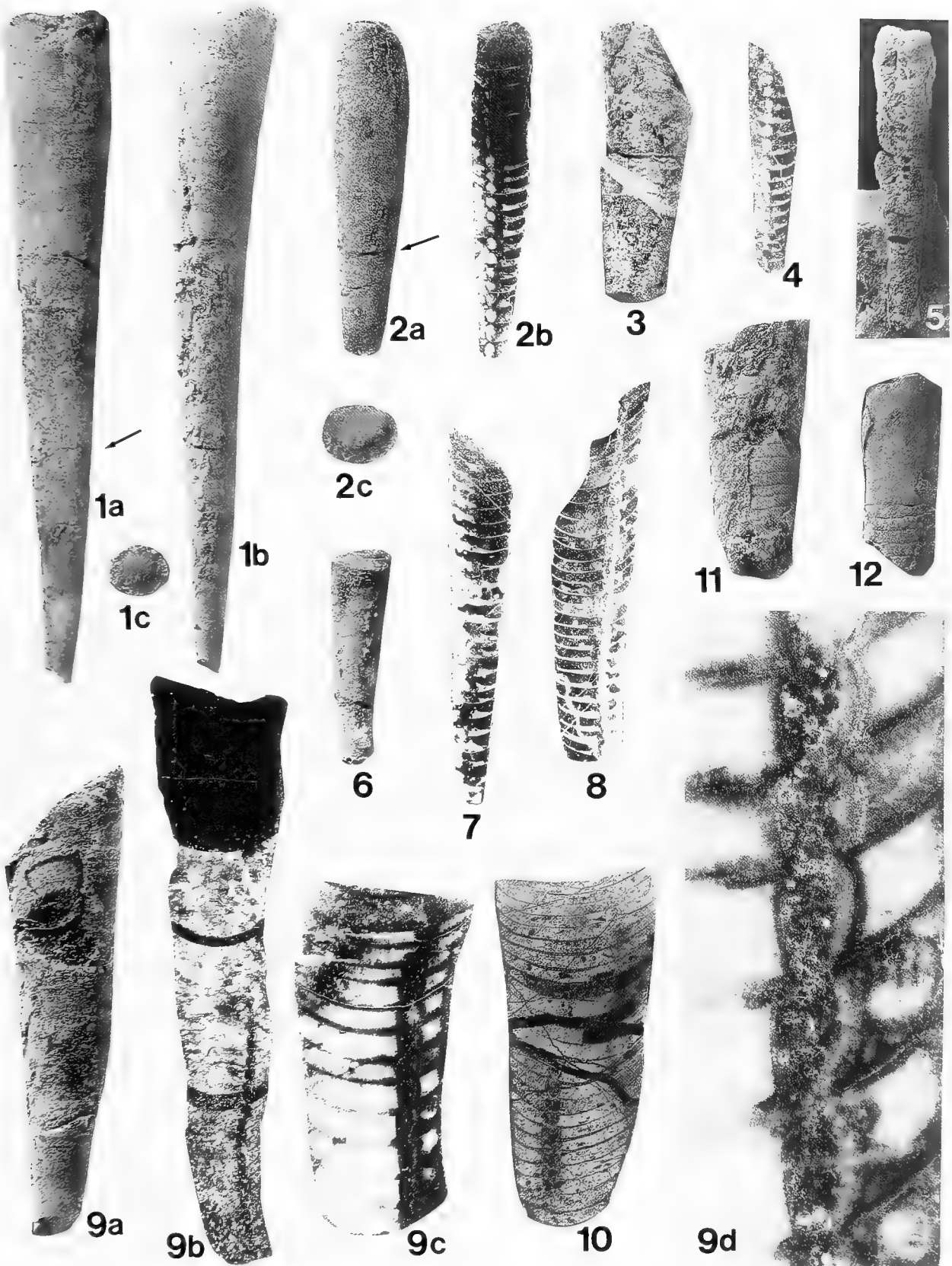
Armenoceras cf. *robustum* (Kobayashi and Matsumoto). Chen, 1983, p. 122, pl. 2, figs. 5, 6.

Wutinoceras robustum (Kobayashi and Matsumoto). Stait and Burrett, 1982, p. 194, figs. 2A–L

Material.—Two phragmocones, KPE20206, 20207 from the middle part of the Maggol Formation of Sanaegol at loc. SN712.

Diagnosis.—Siphuncle eccentric, close to venter, broad; siphuncular segments nummuloidal, highly expanded; thickened connecting ring; septal brims longer than necks, varying from recumbent to slightly hooked, nearly touching the septa only at their tip; reticulate canal system; episepal and hyposeptal deposits present.

Figure 8. 1–8. *Ormoceras cricki* Kobayashi, 1934. All collected from SN741. 1a–c. Nearly complete conch without apical portion, KPE20231, $\times 1.5$, 1a: ventral view, 1b: lateral view, venter on right, 1c: septal view at position indicated by arrow given in 1a. 2a–c. Partial phragmocone, KPE20232, $\times 1.5$, 2a: ventral view, 2b: longitudinal section, venter on left, showing well developed episepal deposits, 2c: septal view at position indicated by arrow given in 2a. 3. Partial phragmocone, KPE20237, ventral view, $\times 2$. 4. Partial phragmocone, KPE20235, longitudinal section, venter on left, $\times 1.5$. 5. Partial phragmocone, KPE20233, ventral view, $\times 1.5$. 6. Partial phragmocone, KPE20245, dorsal view, $\times 1.5$. 7. Partial phragmocone, KPE20234, longitudinal section in slightly askew dorsoventral direction, $\times 1.5$. 8. Partial phragmocone, KPE20244, dorsoventral section, venter on right, $\times 1.5$. 9–12. *Ormoceras weoni* sp. nov. All collected from SN741. 9a–d. Adoral phragmocone and contiguous partial body chamber, holotype, KPE20260, 9a: dorsal view, $\times 1$, 9b: longitudinal section, venter on right, acetate peel, $\times 1.5$, 9c: enlarged view of apical portion, $\times 3$, 9d: details of siphuncle and septa, $\times 12$. 10. Partial phragmocone, paratype, KPE20261, longitudinal section, venter on left, acetate peel, $\times 1.5$. 11. Partial phragmocone, paratype, KPE20265, showing transverse septal sutures, $\times 1.5$. 12. Partial phragmocone and contiguous body chamber, paratype, KPE20264, shell exfoliated, showing transverse septal sutures, $\times 1.5$.



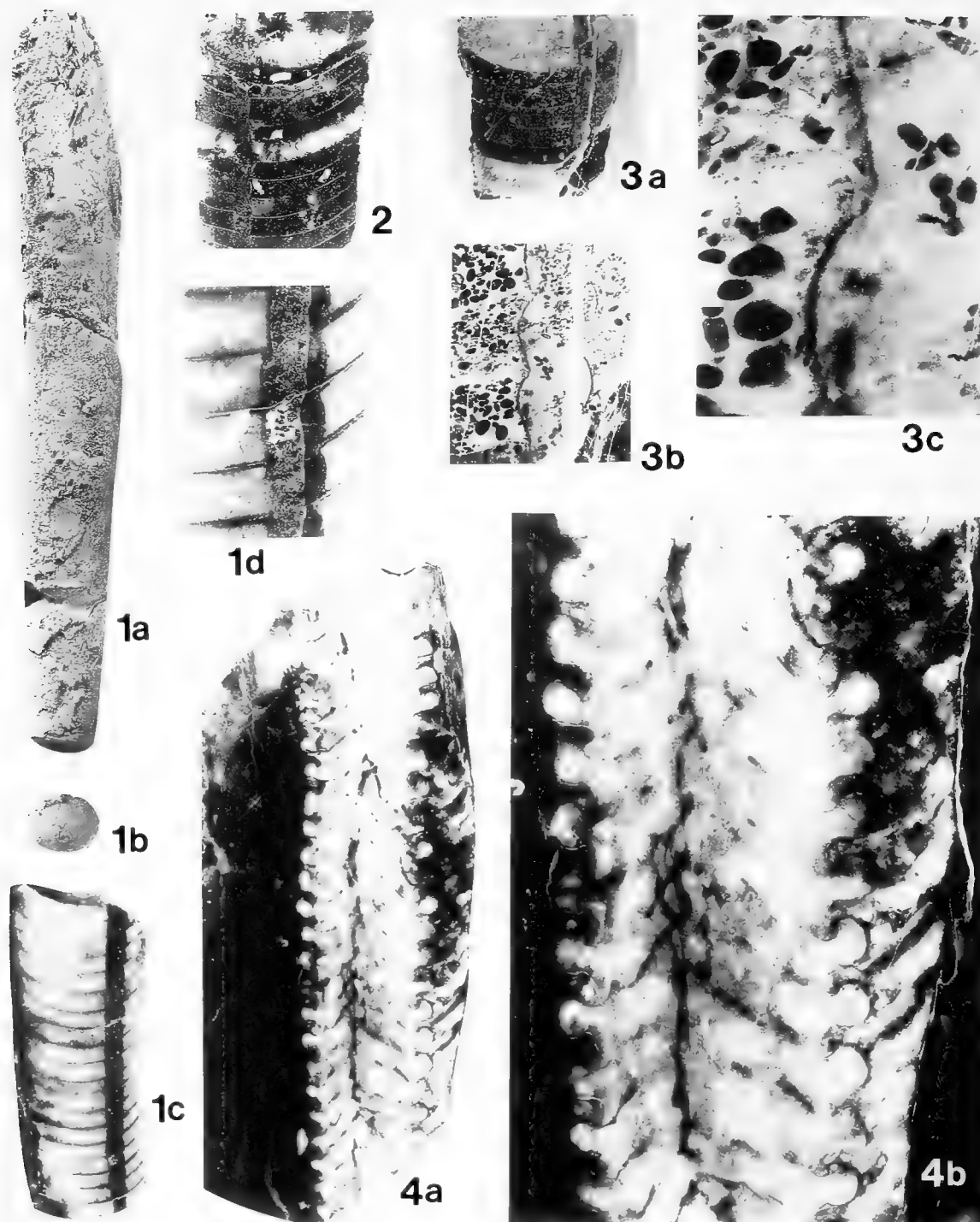


Figure 9. 1-3. *Ormoceras weoni* sp. nov. All collected from SN741. 1a-d. Adoral phragmocone and contiguous body chamber, paratype, KPE20262, 1a: ventral view, body chamber somewhat distorted, $\times 1$, 1b: septal view of apical end, showing position of the siphuncle, $\times 1$, 1c: dorsoventral section, venter on right, $\times 2$, 1d: details of siphuncular structure, showing endosiphuncular linings on ventral side, $\times 7$. 2. Partial phragmocone, paratype, KPE20267, dorsoventral section, venter on left, $\times 2.2$. 3a c. Partial phragmocone, paratype, KPE20263, 3a: dorsoventral section, venter on right, $\times 2$, 3b: detail of siphuncle, $\times 7$, 3c: enlarged view of cyrtochaonitic septal neck, $\times 30$. 4a, b. *Polydesmia* sp. cf. *P. canaliculata* Lorenz, 1906. partial phragmocone, KPE20321, loc. SN720, 4a: longitudinal section, $\times 1$, 4b: enlarged view of siphuncular structure, showing triangular interseptal cavities on the adoral side of septa and steeply inclined radial canals, $\times 5$.

Description.—Large-sized longiconic orthocones with well defined reticulate canal system.

KPE20206 (Figures 6–2 and 10–1a, b), a partial phragmocone with apical end, 115 mm long consisting of 10 siphuncular segments including initial chamber; presumably subcircular in cross section; cameral portion of apical part mostly lost during taphonomic process; siphuncle eccentric, its width broad, occupying nearly a half of conch diameter; siphuncular segments nummuloidal, highly expanded, having a length of 11.2 mm and a width of 27.5 mm at the point of maximum expansion, constricted to 13.7 mm at septal foramen; septa moderately curved, septal depth corresponding to a little less than one and a half times cameral height; septal necks cyrtchoanitic, recurved but free; septal brims longer than necks, varying from recumbent to slightly hooked, nearly touching the septa only at their tip; cameral height rather high, averaging 10.2 mm; connecting ring relatively thick, apically adnate for a long distance, 3.8 mm to adoral surface of septum, just meeting the septal brims adorally; siphuncular deposits of annulosiphonate type, canal system forming reticulate structure, narrow radial canals branched off from irregularly arranged central canal entering to the midpoint of perispatium; episeptal and hyoseptal deposits well developed; shell surface unknown.

KPE20207 (Figures 10–2a, b), represented by a partial phragmocone with one side crushed; a gastropod belonging to *Pagodispira* (?) detected in a camera in cross section (indicated by arrow, see Figure 10–2b); conch somewhat flattened and siphuncle slightly elliptical in cross section; siphuncle eccentric, close to venter; siphuncular segments uniform in dimension, 8.5 mm long and 23.3 mm in maximum diameter within camerae, pinched to 13.1 mm at the septal necks; posterior area of adnation moderately broad, 3.2 mm; central canal sigmoidally curved in longitudinal direction, its width ranging from 1.6 mm to 3.5 mm while radial canal is narrow, 0.4 mm or less, radially distributed bunches of annulosiphonate deposits in cross section of adoral end.

Remarks.—The present species is similar to *Wutinoceras foerstei* (Endo) from the Lower Ordovician Wuting Formation of South Manchuria (Endo, 1930, p. 208, pl. 60, figs. 1A–C) in ectosiphuncular structure and reticulate canal system, but the latter differs from the former in having a more ventrally positioned siphuncle and less cameral deposits. This species may be allied to *Wutinoceras logani* Flower from the Table Head Formation of Newfoundland (Flower, 1968, p. 8, pl. 10, figs. 1–3; pl. 11, figs. 1–7) in the large-sized conch and strongly flattened siphuncular segments, but the former is distinguished from the latter in having more thickened cameral deposits and less recumbent septal brims.

This species is also similar to *Wutinoceras remotum* Chen from the Lower Ordovician, lower part of Jiacun Group of Nielamu County, China (Chen, 1975, p. 274, pl. 1, figs. 7, 8) in the mode of endosiphuncular and cameral deposits, but the latter differs from the former in the longer septal necks and much narrower siphuncular segments.

Occurrence.—In addition to the present materials, this species is known from the Tofangian strata in the vicinity of Nanpiano Coalmine, Nanpiano County, Liaoning Province, South Manchuria (Kobayashi and Matsumoto, 1942) and the Lower Ordovician Lower Setul Limestone on Pulau Langgun of the Langkawi Islands, Malaysia (Stait and Burrett, 1982).

Wutinoceras sp.

Figures 10–3a–d

? *Wutinoceras* sp. Zhu and Li, 1996, pl. 1, fig. 11.

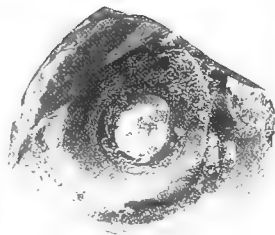
Material.—Partial phragmocone, KPE20202 from loc. SN713.

Description.—Medium-sized orthocone, preserved phragmocone 60 mm long, its expansion rate not measured owing to secondary deformation, conch subcircular in cross section; siphuncle central, large, 11.5 mm in maximum diameter, occupying about one-third of conch diameter; siphuncular segments strongly nummuloidal, 4.2 mm in length and 11.5 mm in maximum diameter at mid-portion within camerae, contracting to 6.6 mm at septal foramen; septa moderately concave adorally, septal depth one and a half times cameral height, septal necks cyrtchoanitic, strongly recurved, septal brims far longer than necks, its end adnate to the adapical surface of septum, especially in juvenile stage, but not adnate in later stage; connecting ring adnate for a relatively long distance to adoral surface of septum dorsally, but free ventrally, just meeting the tip of septal brim; suture slightly sloping from venter to dorsum, but transverse when viewed from dorsal side; camera about 4.3 mm high, 8 camerae preserved in a partial conch 37 mm in length; annulosiphonate deposits well developed (Figures 10–3c, d), annuli embracing the inner margin of septa at septal necks, gradually decreasing adorally in bulk, its shape asymmetrical in longitudinal section, more concentrated to the adoral side, adjacent annuli in contact with each other, remaining spaces forming radial canal, which branches off from much broader central canal, in some cases, radial canal divided into two branches and entering in perispatium; camerae filled with episeptal and hyoseptal deposits only on ventral side, also deposits in ventral camera forming pseudoseptum at mid-portion of camera joining to radial canal.

Figure 10. 1, 2. *Wutinoceras robustum* (Kobayashi and Matsumoto, 1942). 1a, b. Partial phragmocone, KPE20206 from SN712, 1a: longitudinal polished section of an originally weathered specimen, $\times 1$, 1b: details of septal necks and reticular canal system, acetate peel, $\times 2.4$. 2a, b. Partial phragmocone, KPE20207 from SN712, $\times 1$, 2a: longitudinal section, venter on left, 2b: cross section at the adapical end, venter down. Arrow indicates a gastropod, *Pagodispia* (?) sp. 3a–d. *Wutinoceras* sp. partial phragmocone, KPE20202 from SN713, 3a: lateral view, venter on right, $\times 1$, 3b: septal view of the apical end, venter down, showing position of the siphuncle, $\times 1$, 3c: longitudinal section, venter on left, showing the annulosiphonate deposits, $\times 1$, 3d: details of siphuncular structure, acetate peel, showing free septal necks, but tip of septal brims adnate to the adapical surface of the septum, and well-developed annulosiphonate deposits, $\times 5$. Abbreviations in Figure 3d: an; annulus, cc; central canal, rc; radial canal.



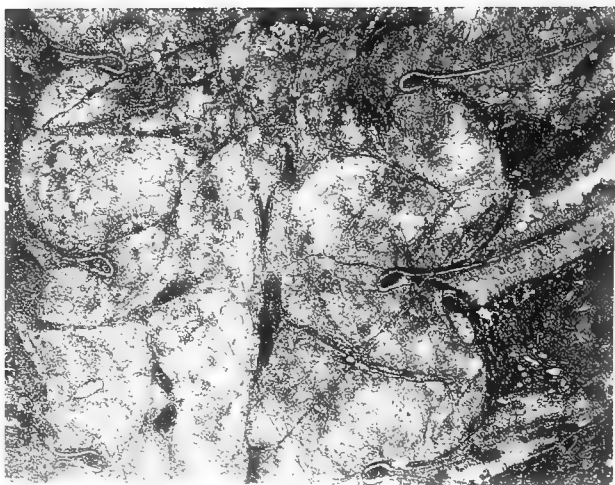
1a



3b



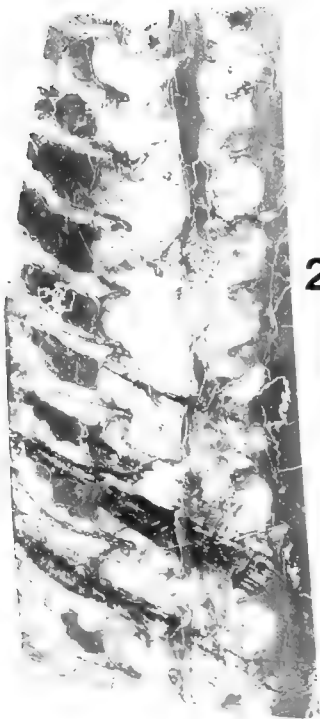
2b



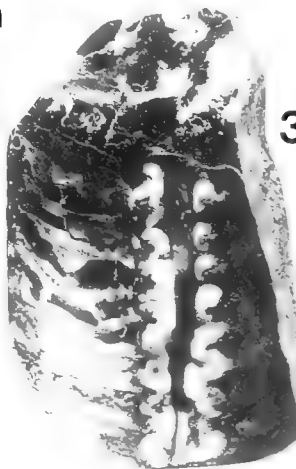
1b



3a



2a



3c



3d

Remarks.—This species resembles *Wutinoceras giganteum* Flower from the early Middle Ordovician Table Head Limestone of Newfoundland (Flower, 1976, pl. 2, fig. 4; pl. 3, fig. 12; pl. 4, figs. 1, 2; pl. 5, fig. 6) in the nearly central position of the siphuncle, but is distinguished by its more crowded camera, obliquely inclined septal suture and the presence of the well-developed canal system. In the flattened siphuncular segments and recumbent septal necks, this present species is somewhat similar to *Wutinoceras logani* Flower from the Table Head Limestone, Newfoundland (Flower, 1968, p. 8, pl. 10, figs. 1–3; pl. 11, figs. 1–7), but differs by its more undulating central endosiphuncle and thicker mural-episepal deposits.

Wutinoceras lui Chang from the Inner Mongolia (Chang, 1959, pl. 2, fig. 3; pl. 3, fig. 5) is also allied to this species, but the former differs from the latter in its eccentric siphuncle and less flattened siphuncular segments. Furthermore, the present species is allied to *Wutinoceras shihuigouense* Chang from the upper part of the Lower Ordovician Tochuanshan Limestone, Shihuigou, Chinghai (Chang, 1965, p. 352, pl. 1, fig. 4) in the subcentral position of the siphuncle and the constant relation of the septa and segments, but in *W. shihuigouense*, the septa are more steeply inclined and the connecting ring is rather uneven. *Wutinoceras* sp. from the Lower Ordovician Xiamajiagou Formation of Southern Jilin, China (Zhu and Li, 1996, pl. 1, fig. 11) may be compared to the present species in its free septal necks and somewhat broader area of adnation.

Occurrence.—Known only from the middle part of the Maggol Formation of Sanaegol.

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Erratum

In the article by Amano, Lutaenko and Matsubara (*Paleontological Research*, Vol. 3, No. 2), a sentence below should be included in the figure caption of Figure 4 on page 98.

6a, b : *Macoma (Rexithaerus) hokkaidoensis* Amano and Lutaenko, sp. nov., JUE no. 15654 (Paratype), Oshamanbe (Recent).

行 事 予 定

- ◎ 2000 年年会・総会は、2000 年 1 月 28 日 (金)～1 月 30 日 (日) に「早稲田大学」で開催されます。一般講演の申し込み締め切りは 1999 年 12 月 3 日です。1 月 28 日にシンポジウム「白亜紀の炭素循環と生物多様性の変動：世話人・平野弘道・坂井 卓・松川正樹・中森 亨・西 弘嗣・利光誠一・斎木健一・長谷川卓」が行われます。
- ◎ 第 149 回例会 (開催予定時期：2000 年の 6 月末頃) には、「群馬県立自然史博物館」から開催申し込みがありました。
- ◎ 1999 年総会で、2001 年からの年会・総会と例会の開催時期の変更が決定されました。年会・総会は 6 月下旬から 7 月の初め頃 (現在の例会の開催時期)、例会は 1 月下旬から 2 月の初め頃 (現在の年会・総会の開催時期) 開催されます。開催を計画されている機関がありましたら、行事係までお申し込み下さい。

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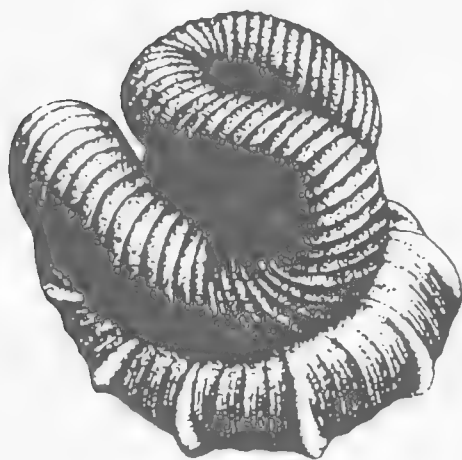
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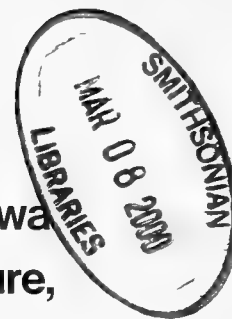
Cover : Idealized sketch of *Nipponites mirabilis* Yabe, a Late Cretaceous (Turonian) nostoceratid ammonite. Various reconstructions of the mode of life of this species have been proposed, because of its curiously meandering shell form (after T. Okamoto, 1988).

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Middle Miocene deep-water molluscs from the Arakawa Formation in the Iwadono Hills area, Saitama Prefecture, central Japan

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Abstract. Twenty-five molluscan taxa were identified from three localities of the lower Middle Miocene Arakawa Formation in the Iwadono Hills area, Saitama Prefecture, central Japan. This fauna consists of two types of assemblage (protobranch-dominant and septibranch-dominant) and is inferred to represent a deep-water fauna (bathyal depths) on the basis of its taxonomic structure. Similarities in generic composition between the molluscan fauna of the Arakawa Formation and that of the bathyal zone in modern Sagami Bay suggest that the marine climate during the Arakawa deposition is comparable with that of the intermediate water of Sagami Bay. One new species, *Neilonella tsukigawaensis*, is described herein, and the stratigraphic relationship between the Arakawa and the overlying Goudo Formation is briefly mentioned.

Key words: Arakawa Formation, deep water molluscan fauna, Iwadono Hills, Miocene, intermediate water

Introduction

Mollusc-bearing marine Miocene strata are exposed in the Iwadono Hills area, located in the eastern margin of the Kanto Mountains, Saitama Prefecture, central Japan (Figure 1-A). They are stratigraphically divided into the Arakawa, Goudo, Syougunzawa, Hatoyama, and Imazyuku Formations in ascending order (Majima, 1989). Molluscan fossils from the Goudo and Syougunzawa Formations have been listed and partly illustrated by Hatai and Masuda (1962) and Majima (1989), but there has not been any paleontological work on the molluscan fauna from the Arakawa Formation in the Iwadono Hills area.

During my field survey in the Iwadono Hills area from 1993 to 1994, approximately one hundred specimens of molluscan fossils were collected from the Arakawa Formation, in which two types of deep-water assemblages were recognized. The purpose of this paper is to report the molluscan fauna of the Arakawa Formation in the Iwadono Hills area and to discuss the inferred paleobathymetry and marine paleoclimate of the formation based on the molluscan faunal analysis.

Geologic setting and age

Miocene strata distributed in the Iwadono Hills area are separated by a fault from Pre-Tertiary metamorphic rocks in the western part and are overlain by the Plio-Pleistocene Monomiyama Formation in the southern part (Figure 1-B).

Koike *et al.* (1985) and Majima (1989) recently studied the geology of the Iwadono area, but their stratigraphic divisions are slightly different from each other (Figure 2). In this paper, I follow Majima's (1989) division because he made it clear that the lowermost Miocene stratigraphic unit in the Iwadono area belongs to the Arakawa Formation (Watanabe *et al.*, 1950), which is widely distributed in the central part of Saitama Prefecture.

The Arakawa Formation in the northern study area is exposed narrowly and sporadically (Figure 1-C). It consists mainly of diatomaceous siltstone and sandy siltstone, both of which commonly contain sand-sized fragments of schist. In this lithological feature, the Arakawa Formation can be distinguished from the other Miocene siltstone-dominant formations in the Iwadono area. Although partial sections were measured at the place where the megafossils were collected, structural complexities and poor exposures make it difficult to correlate these sections. The Arakawa Formation is considered to be overlain by the Goudo Formation, which is composed mainly of sandstone and conglomerate, but their stratigraphic relationship is unclear, as will be mentioned.

The geologic age of the Arakawa Formation recently became better defined by means of diatom biostratigraphy. Kurihara (1994MS) obtained for the first time from the formation (Loc. 1 of Figure 1-C and Table 1) a diatom assemblage, which he assigned to the early Middle Miocene *Denticulopsis lauta* Zone (NPD 4A) of Akiba's (1986) Neogene North Pacific Diatom Zonation (Horiuchi and Yanagisawa, 1994).

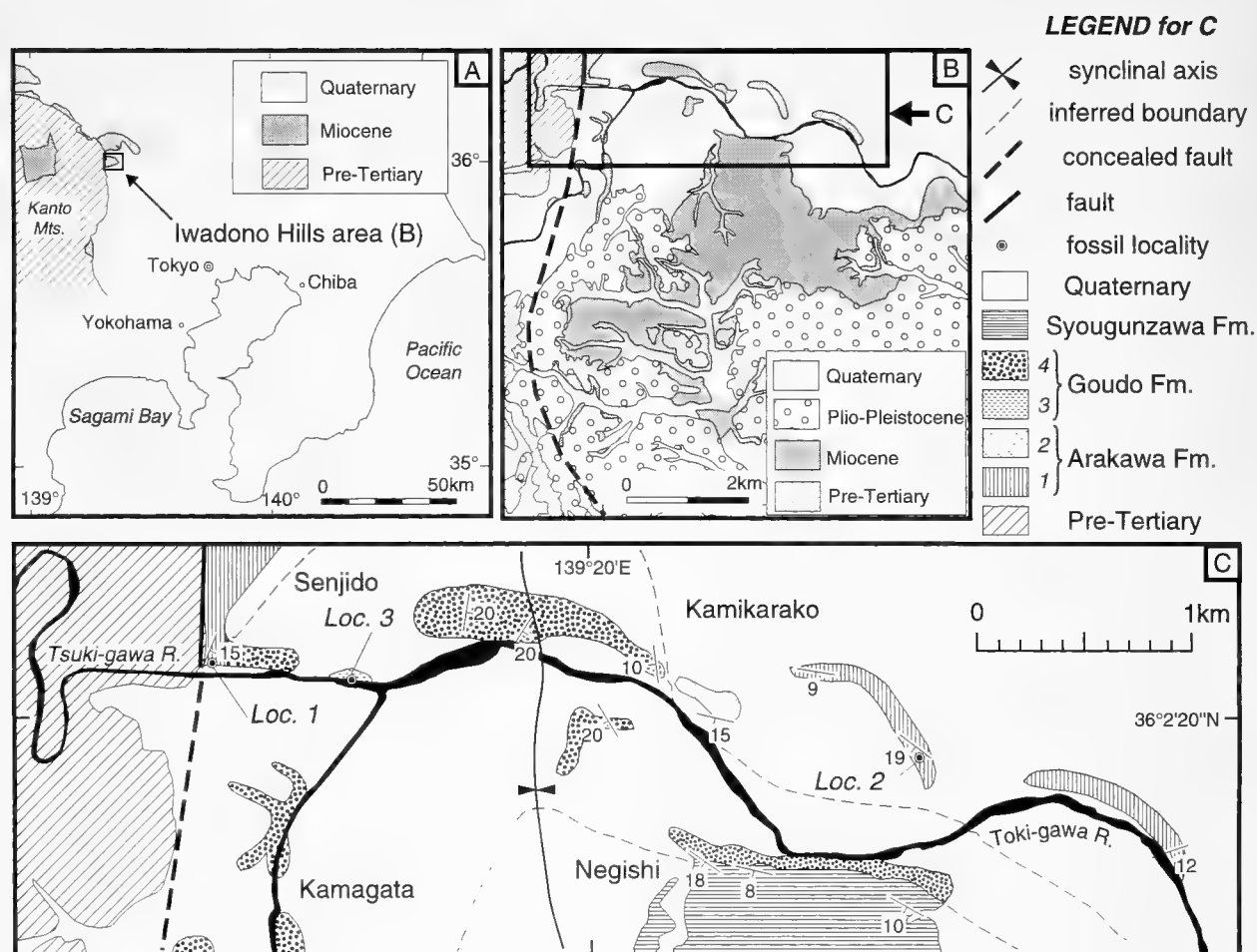


Figure 1. (A) Index map showing the Iwadono Hills area, and the geologic sketch map of eastern margin of the Kanto Mountains. (B) Geologic sketch map of the Iwadono area. (C) Geologic map of the northern part of the Iwadono area with the fossil localities. Legend: 1, diatomaceous siltstone; 2, sandy siltstone; 3, conglomerate consisting mainly of sandy siltstone boulders; 4, sandstone and conglomerate.

| Koike <i>et al.</i> (1985) | | | Majima (1989) |
|----------------------------|----------------|-------------------------|----------------|
| Tokigawa Group | Ohashi Fm. | Imajuku Ss. Mm. | Imazyuku Fm. |
| | | Hatoyama Ss. & Slt. Mm. | Hatoyama Fm. |
| | Iwadono Fm. | Shogunzawa Slt. Mm. | Syogunzawa Fm. |
| | | Negishi Ss. Mm. | Goudo Fm. |
| | | Godo Cgl. Mm. | |
| | unconformity | | unconformity? |
| | Kamikarako Fm. | | Arakawa Fm. |

Figure 2. Comparison of stratigraphic divisions of the Miocene in the Iwadono Hills area by recent workers. Fm., Formation; Mm., Member; Cgl., Conglomerate; Ss., Sandstone; Slt., Siltstone.

According to Y. Yanagisawa (per. com.), the formation in the Iwadono area is assigned for the most part to NPD 4A, with the lowermost part extending to the latest Early Miocene *Crucidenticula kanayae* Zone (NPD 3A). Therefore, the Arakawa Formation in the Iwadono area ranges from the uppermost Lower to lower Middle Miocene in age. The molluscan fossils treated in this paper cooccurred with a diatom assemblage assigned to the middle part of NPD 4A, which is characterized by the occurrence of the very short-ranging species *Cavitatus lanceolatus*. According to the latest age estimation of diatom datum levels by Yanagisawa and Akiba (1998), NPD 4A with *C. lanceolatus* ranges from 15.6 to 15.2 Ma. The Goudo Formation yields larger foraminifers including *Lepidocyclina* sp., which also suggest a lower Middle Miocene (Blow's N. 8-9) age (Majima, 1989).

Table 1. List of the diatom fossils from the Arakawa Formation (Loc. 1) and from sandy siltstone boulders in the Goudo Formation (Loc. 3) (identified by Y. Yanagisawa). Numbers indicate those of individuals for species that occur from 100 individuals selected at random. + indicate recognizable species.

| Sample locality | Loc. 1 | Loc. 3 |
|---|--------|--------|
| Sample number | Sg 3 | lwd 9 |
| Diatom zone | 4A | 4A |
| <i>Actinocyclus ingens</i> f. <i>ingens</i> (Rattray) Whiting et Schrader | 5 | 16 |
| A. <i>ingens</i> f. <i>nodus</i> (Baldauf) Whiting et Schrader | + | 1 |
| A. <i>ingens</i> f. <i>planus</i> Whiting et Schrader | 6 | 13 |
| A. <i>octonarius</i> Ehrenberg | — | 1 |
| <i>Actinoptychus senarius</i> (Ehrenberg) Ehrenberg | + | 3 |
| <i>Cavitatus exiguus</i> Yanagisawa et Akiba | 1 | 2 |
| C. <i>jouseanus</i> (Sheshukova) Williams | + | 2 |
| C. <i>lanceolatus</i> Akiba et Hiramatsu | 5 | 1 |
| C. <i>linearis</i> (Sheshukova) Akiba et Yanagisawa | + | — |
| C. <i>miocenicus</i> (Schrader) Akiba et Yanagisawa | — | 1 |
| <i>Cestodiscus</i> sp. (concave) | + | — |
| <i>Coscinodiscus lewicianus</i> Greville | + | 1 |
| C. <i>marginatus</i> Ehrenberg | 1 | — |
| C. <i>perforatus</i> Ehrenberg | — | 1 |
| <i>Crucidenticula kanayae</i> var. <i>kanayae</i> Akiba et Yanagisawa | + | — |
| <i>Delphineis miocenica</i> (Schrader) Andrews | 1 | — |
| <i>Denticulopsis ichikawae</i> Yanagisawa et Akiba | 8 | 3 |
| D. <i>lauta</i> (Bailey) Simonsen | 8 | 3 |
| D. cf. <i>okunoi</i> Yanagisawa et Akiba | + | — |
| Girdle view of <i>D. lauta</i> group | 7 | + |
| <i>Hemiaulus bipons</i> (Ehrenberg) Grunow in Heurck | + | — |
| <i>Ikebea tenuis</i> (Trun) Akiba | + | — |
| <i>Nitzschia challenger</i> Schrader | + | — |
| <i>Paralia sulcata</i> (Ehrenberg) Cleve | 13 | 11 |
| <i>Planifolia tribranchiata</i> Ernissee | — | 1 |
| <i>Stellarima microtrias</i> (Ehrenberg) Hasle et Sims | 1 | — |
| <i>Stephanopyxis</i> spp. | 1 | 2 |
| <i>Thalassionema</i> cf. <i>hirosakiensis</i> (Kanaya) Schrader | + | — |
| T. <i>nitzschoides</i> (Grunow) H. et M. Peragallo | 44 | 38 |
| <i>Thalassosira leptopus</i> (Grunow) Hasle et Fryxell | + | — |
| <i>Thalassiothrix logissima</i> Cleve et Grunow | + | + |
| Total number of valves counted | 100 | 100 |
| Resting spore of <i>Chaetoceros</i> | 18 | 12 |

Remarks on the stratigraphic relationship between the Arakawa Formation and the overlying Goudo Formation

The stratigraphic relationship between the Arakawa and Goudo Formations is unclear because of the lack of a boundary outcrop, except for a fault contact.

Previous workers pointed out that the Arakawa Formation might be unconformably overlain by the Goudo Formation primarily on the basis of structural differences (Koike *et al.*, 1985) or the presence of pebbles presumably derived from the Arakawa Formation in the Goudo Formation (Majima, 1989).

Recently, I found new evidence by which to consider the stratigraphic relationships of the two formations.

A conglomerate facies including abundant sandy siltstone boulders (more than 2 m in maximum diameter) is observed in the very coarse-grained sandstone matrix of the Goudo Formation at Loc. 3 (Figures 1–C and 3–C). The boulders are considered to have been derived from the Arakawa Formation, because: (1) the sandy siltstone boulders commonly contain sand-sized fragments of schist; this lithofacies characterize the Arakawa Formation as mentioned before; (2) the sandy siltstone lithology of the boulders resembles that of the Arakawa Formation exposed at Kamikaraka (see Figure 1–C); (3) the boulders are too large to have been transported from outside the Iwadono area, and (4) the diatom assemblage in the boulders is assigned in age to Akiba's NPD 4A, which is the same as the Arakawa Formation (Table 1). Although the exact boundary between

the Arakawa and Goudo Formations could not be observed at Loc. 3, the facies including the boulders may represent a basal unit of the Goudo Formation which presumably covers the Arakawa Formation with an erosional contact. However, it is difficult to conclude that the relationship between these two formations is an unconformity, because of the lack of chronological data indicating the time gap between them.

Occurrence of molluscs

Molluscan fossils treated in this paper were collected from the diatomaceous siltstone of the Arakawa Formation (Locs. 1, 2) and from the sandy siltstone boulders in the Goudo Formation (Loc. 3) (Figure 1-C). The boulders are considered to have been derived from the Arakawa Formation as mentioned before, thus the molluscan fossils contained in the boulders are treated as derived from the Arakawa Formation. Columnar sections showing the sampling hori-

zon of Locs. 1 and 2 are shown in Figures 3-A and B, respectively.

Preservation of molluscs from the Arakawa Formation is generally poor and varies in relation to their enclosing lithology. Molluscan shells from the diatomaceous siltstone at Locs. 1 and 2 are completely dissolved and are preserved as molds, whereas those from the sandy siltstone at Loc. 3 often retain their shell material. Molluscan fossils from the diatomaceous siltstone have suffered more significant post-depositional deformation than those from the sandy siltstone.

The mode of fossil occurrence remains almost constant at the three localities. Molluscan fossils are sporadically distributed in random orientation within the intensively bioturbated massive silty matrix. The shells generally do not show signs of post-mortem wear or breakage. Most bivalve shells are disarticulated (Table 2). The intensively bioturbated sediments suggest that burrowing animals reworked the shells, in which case the empty bivalve shells may have been disarticulated by bioturbation and not retained their life position. The sporadic occurrences of the shells and their showing no sign of abrasion and breakage suggest that the molluscan assemblage is essentially parautochthonous.

Molluscan assemblages

Six gastropods, one scaphopod and 18 bivalves were identified from the Arakawa Formation in the Iwadono area (Table 2).

On the basis of occurrence of the characteristic species, two types of molluscan assemblages are recognized. The essentially parautochthonous nature of the molluscan fossils suggests that these assemblages may represent former benthic communities. Characteristics of specific compositions of each assemblage are described below.

Type I: *Myonera osawanoensis* assemblage

This assemblage is recognized in diatomaceous siltstone at Locs. 1 and 2. It is characterized by the dominance of *Myonera osawanoensis*, which accounts for nearly 50% of the total number of the specimens. Commonly associated species are *Portlandia* sp. and *Delectopecten* cf. *peckhami*.

Type II: *Neilonella tsukigawaensis* assemblage

This assemblage is recognized in massive sandy siltstone boulders at Loc. 3. It is characterized by the dominance of *Neilonella tsukigawaensis* sp. nov., which accounts for about 25% of the total number of the specimens. Subdominant species are *Portlandia* sp. and *Orectospira* sp.

Paleobathymetry

For the paleobathymetric interpretation of Cenozoic molluscan faunas, the taxonomic structure method is useful because it can discriminate between shallow- (less than 200 m) and deep-water (greater than 200 m) faunas. This method was developed by Hickman (1974, 1984) and is based on the observation that the percent composition of species representing major taxonomic division of the molluscan group changes with depth in modern major regional faunas.

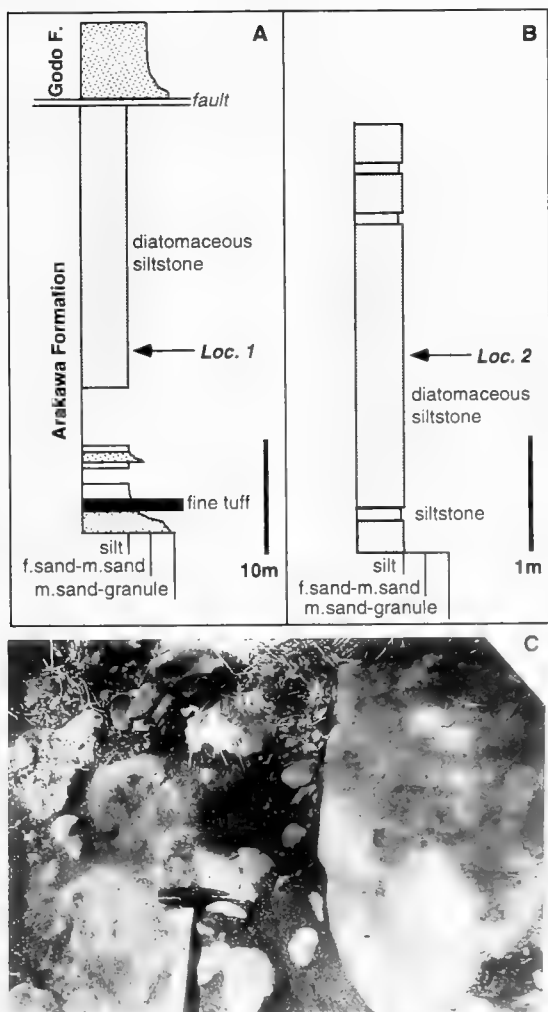


Figure 3. Columnar sections showing the sampling horizon of Locs. 1 (A) and 2 (B). Field photo showing mode of occurrence of sandy siltstone boulders at Loc. 3 (C).

Table 2. List of the molluscan fossils from the Arakawa Formation. Numbers represent those of individuals. For bivalves, the numbers naked and in the parenthesis represent those of disarticulated and articulated valves, respectively.

| Assemblage type | I | | II |
|---|--------|--------|--------|
| Locality | Loc. 1 | Loc. 2 | Loc. 3 |
| <i>Puncturella</i> sp. | 1 | — | — |
| <i>Bathybembix</i> ? sp. | 1 | — | — |
| <i>Bolma</i> ? sp. | — | — | 1 |
| <i>Orectospira</i> sp. | — | — | 4 |
| <i>Epitonium</i> sp. | — | — | 1 |
| <i>Ancistrolepis</i> sp. | — | — | 2 |
| <i>Fissidentalium</i> sp. | — | — | 1 |
| <i>Acila</i> sp. | — | — | 1 |
| <i>Bathymalletia chitensis</i> Shikawa and Kase | 1 | — | — |
| <i>Neilonella isensis</i> Shibata | — | — | 2 |
| <i>Neilonella tsukigawaensis</i> sp. nov. | — | — | (2) 8 |
| <i>Tindaria</i> ? sp. | — | 3 | — |
| <i>Nuculana</i> (<i>Testylea</i>) sp. | — | — | 1 |
| <i>N. (Crassoleda) aff. pennula</i> (Yokoyama) | — | 2 | 2 |
| <i>Portlandia</i> sp. | 4 | 10 | 7 |
| <i>Acar</i> sp. | — | — | 1 |
| <i>Delectopecten</i> cf. <i>peckhami</i> (Gabb) | 1 | 2 | — |
| Anomiidae gen. et sp. indet. | 1 | — | 1 |
| <i>Lucinoma</i> sp. | — | — | 3 |
| <i>Conchocele</i> sp. | — | — | 1 |
| <i>Macoma</i> ? sp. | — | — | 1 |
| <i>Halicardia</i> sp. | — | — | 1 |
| <i>Cuspidaria</i> sp. | 1 | — | — |
| <i>Cardiomya mitsuganoensis</i> Shibata | — | 2 | — |
| <i>Myonera osawanoensis</i> (Tsuda) | (6)11 | (3)14 | — |

As Hickman (1984) has emphasized, the taxonomic structure method is a tool for analyzing not individual assemblages but entire faunas. I examined the taxonomic composition of the whole bivalve fauna of the Arakawa Formation in the Iwadono area. The composition of the gastropod fauna was not examined because of the very low species diversity of gastropods in the Arakawa Formation.

Figure 4 illustrates the taxonomic composition of the bivalve fauna of the Arakawa Formation and those from the modern shelf, bathyal, and abyssal zones for comparisons. As shown in this figure, the proportions of protobranchs and heterodonts in modern shallow- and deep-water faunas are remarkably reversed. Hickman (1984) used the predominance of protobranchs over heterodonts as an indicator of deep water for paleobathymetric interpretation of Paleogene molluscan faunas. The Arakawa bivalve fauna is clearly indicative of deep water in the remarkable predominance of protobranchs. Another distinct feature in the taxonomic composition of the Arakawa bivalve fauna is the subdominance of septibranchs, which is also characteristic of deep water in modern faunas. Proportionally, the structure of the Arakawa bivalve fauna is most similar to that of the modern abyssal fauna. However, this similarity is superficial because the taxonomic structure method is not able to discriminate between bathyal and abyssal faunas.

Next, I examined the compilations of modern bathymetric ranges of the constituent genera of the Arakawa fauna on the basis of the distribution data of Recent molluscs by Higo and Goto (1993). As a result, it became clear that both Type-I and -II assemblages contain genera restricted to bathyal depths such as *Myonera* and *Halicardia*, respectively and that the other genera have a wide range taking in the sublittoral to bathyal zones. Bathymetric ranges of *Myonera* and *Halicardia* in the modern northwestern Pacific are 400–900 m and 400–1,500 m, respectively (Higo and Goto, 1993). There is no genus restricted to the sublittoral zone. Therefore, both Type-I and -II assemblages can be considered to represent a fauna of bathyal depths. It is difficult to discuss in more detail the paleobathymetry of both assemblages and their bathymetric relationship with the present data. Both Type-I and -II assemblages are dominated by proto-branch bivalves in terms of species number and are comparable with the Protobranch Communities, one of the six Cenozoic deep-water molluscan community types of Hickman (1984). There is, however, a difference between Type-I and -II in terms of major taxonomic groups of dominant species. The type-II assemblage clearly belongs to the Protobranch Communities in the dominance of a proto-branch bivalve, *Neilonella tsukigawaensis* sp. nov. On the other hand, the Type-I assemblage differs from the typical Proto-

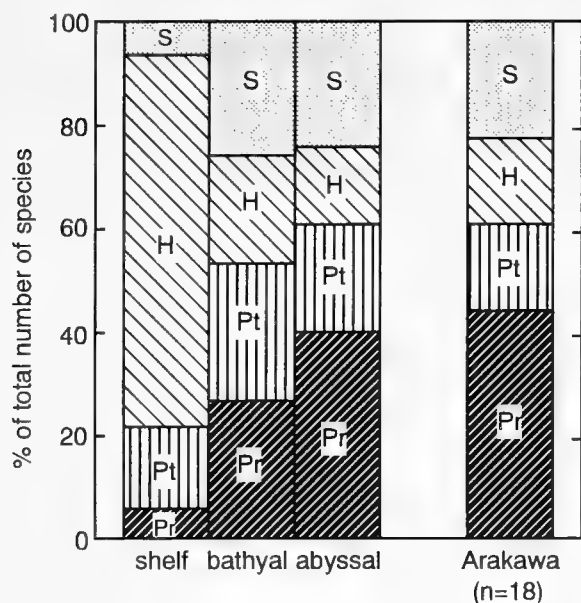


Figure 4. Taxonomic composition of the bivalve fauna of the Arakawa Formation and those from modern shelf (less than 200 m), bathyal (200–2,000 m) and abyssal (greater than 2,000 m) zones for comparisons (after Hickman, 1984). Pr, Proto-branches; Pt, Pteriomorphs; H, heterodonts; S, septibranchs. Letter n represents the number of species.

branch Communities in the dominance of a septibranch bivalve, *Myonera osawanoensis*. Such an assemblage dominated by a septibranch bivalve may be distinguishable from Hickman's six Cenozoic deep-water molluscan community types and may represent a new one, the Septibranch Communities.

Marine paleoclimate

The marine paleoclimatic aspect of the Arakawa fauna is

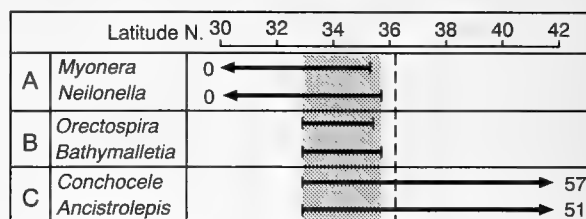


Figure 5. Latitudinal range of the selected genera of the Arakawa fauna in the modern northwestern Pacific. Overlapped area of A, B and C-type genera is indicated by shade. Dotted line represents the latitude of the Iwadono Hills area.

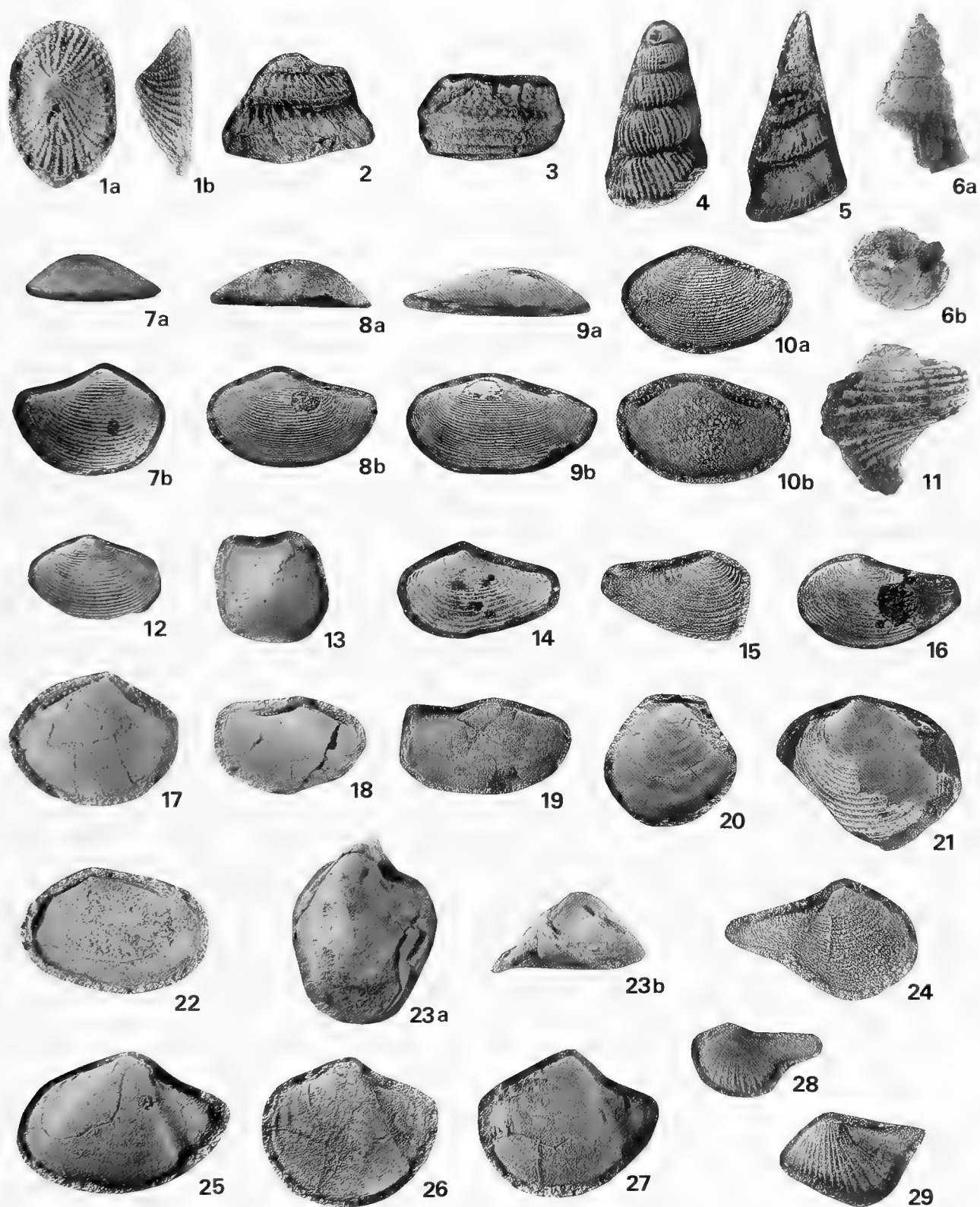
here inferred on the basis of the observed latitudinal ranges of the constituent genera in the modern northwestern Pacific by Kuroda and Habe (1952) and Higo and Goto (1993).

The Arakawa fauna contains several genera that show distinct latitudinal distributions and which can be grouped into three types on the basis of their distribution patterns; namely, A, B, and C-types (Figure 5). The A-type genera are widely distributed to the south of Lat. 36°N, the B-type are restricted between 33° and 36°N, and the C-type are widely distributed to the north of 33°N. The A-type genera, *Myonera* and *Neilonella*, can be regarded as southern elements, and the B-type genera, *Orectospira* and *Bathymalletia*, are nearly equivalent to the Southwestern Japonic elements of Nobuhara (1993). The C-type genera, *Ancistrolepis* and *Conchocele*, are known as northern elements, because their main distribution is in northern sea areas (Okutani, 1968).

In the Pacific coast of Japan, the cooccurrence of the three types of genera is now restricted to deep water of Lat. 33° to 36°N. According to Okutani's (1968) study of the deep-water molluscan fauna in Sagami Bay (approximately Lat. 35.2°N; see Figure 1-A), the cooccurrence of the three types of genera is typically recognized at depths of 400 to 1,000 m, where they would be bathed in the intermediate water at 6 to 8°C, and where most of the constituent genera (about 80%) of the Arakawa fauna occur. Such similarities

→ **Figure 6.** (For bivalves, RV and LV are used for abbreviation of right valve and left valve, respectively.) **1a-b.** *Puncturella* sp., Loc. 1, rubber cast, $\times 4$, (a) dorsal view, (b) lateral view, IGUT 11847. **2.** *Bathybembix* ? sp., Loc. 1, rubber cast, $\times 2.5$, IGUT 11848. **3.** *Bolma* ? sp., Loc. 3, rubber cast, $\times 1.5$, IGUT 11849. **4.** *Epitonium* sp., Loc. 3, rubber cast, $\times 2.5$, IGUT 11851. **5, 6a-b.** *Orectospira* sp., Loc. 3, 5, rubber cast, $\times 2$, IGUT 11850 2; 6. $\times 2.3$, (a) lateral view, (b) basal view, IGUT 11850-1. **7a-b, 12.** *Neilonella isensis* Shibata, Loc. 3, $\times 3.5$, 7. RV (a) dorsal view, (b) lateral view, IGUT 11833; 12. LV, IGUT 11832. **8a-b, 9a-b, 10a-b.** *Neilonella tsukigawaensis* sp. nov., Loc. 3, $\times 3.5$, 8. LV, (a) dorsal view, (b) lateral view, IGUT 11834 1, holotype; 9. LV (a) dorsal view, (b) lateral view, IGUT 11834-2, paratype; 10. LV, (a) rubber cast, (b) internal mold, IGUT 11834 3, paratype. **11.** *Ancistrolepis* sp., Loc. 3, $\times 1.5$, IGUT 11852. **13.** *Bathymalletia chitensis* Shikama and Kase, Loc. 1, rubber cast of RV, $\times 2.5$, IGUT 11836. **14, 15.** *Nuculana* (*Crassoleda*) aff. *pennula* (Yokoyama), 14. Loc. 3, LV, $\times 3.5$, IGUT 11839; 15. Loc. 2, rubber cast of RV, $\times 3$, IGUT 11840. **16.** *Nuculana* (*Thestyleda*) sp., Loc. 3, LV, $\times 3$, IGUT 11838. **17.** *Tindaria* ? sp., Loc. 1, internal mold of LV, $\times 4$, IGUT 11835. **18, 19.** *Portlandia* sp., 18. Loc. 2, internal mold of RV, $\times 1.5$, IGUT 11841-1; 19. Loc. 1, internal mold of RV, $\times 1.5$, IGUT 11841-2. **20.** *Delectopecten* cf. *peckhami* (Gabb), Loc. 1, internal mold of RV, $\times 2$, IGUT 11837. **21.** *Lucinoma* sp., Loc. 3, RV, $\times 2$, IGUT 11842. **22.** *Macoma* ? sp., Loc. 3, internal mold of RV, $\times 1.5$, IGUT 11843. **23a-b.** *Halocardia* sp., Loc. 3, RV, $\times 1.5$, (a) undulations and a depressed and triangle shaped rostrum. The shell outline is somewhat variable in the examined specimens as illustrated. **24.** *Cuspidaria* sp., Loc. 1, rubber cast of RV, $\times 3$, IGUT 11844. **25, 26, 27.** *Myonera osawanoensis* (Tsuda), 25. Loc. 2, internal mold of LV, $\times 3$, IGUT 11845-3; 26. Loc. 1, internal mold of LV, $\times 3$, IGUT 11845-2; 27. Loc. 1, internal mold of LV, $\times 3$, IGUT 11845-1.

This species is closely related to *Myonera dautzenbergi* Prasad, 1932, which currently mold of LV, $\times 3$, IGUT 11845-2; 27. Loc. 1, internal mold of LV, $\times 3$, IGUT 11845-1. **28, 29.** *Cardiomya mitsuganoensis* Shibata, Loc. 2, rubber cast of LV, $\times 5$, 28. IGUT 11854-1; 29. IGUT 11854 2.



in the generic composition between the molluscan fauna of the Arakawa Formation and of the bathyal zone in modern Sagami Bay suggests that the marine climate during the Arakawa deposition was similar to that of the intermediate water of modern Sagami Bay.

Systematic paleontology

A new species and another species in a new combination are described in this section. All the illustrated specimens are deposited in the Institute of Geoscience, University of Tsukuba, under the IGUT collection catalogue numbers.

Family Malletiidae

Genus *Neilonella* Dall, 1881

Neilonella tsukigawaensis sp. nov.

Figures 6-8a, b, 9a, b, 10a, b

? *Neilonella* cf. *soyoe* Habe. Shibata in Itoigawa et al., 1974, p. 47-48, pl. 1, fig. 18; Itoigawa et al., 1981, pl. 1, fig. 7; Itoigawa et al., 1982, p. 7.

Type.—The holotype is a left valve (IGUT 11834-1). The paratypes, IGUT 11834-2, 3. All from Loc. 3: a riverside exposure along the Tsuki-gawa River, about 250 m downstream of the Tsuki-gawa Bridge, Senjido, Ranzan-machi, Hiki-gun, Saitama Prefecture.

Diagnosis.—Moderate sized species of *Neilonella*, characterized by its elongate-ovate outline, broad umbo, and surface sculptured all over with densely spaced distinct commarginal ribs.

Description.—Shell moderate in size for the genus, rarely exceeding 10 mm in length, elongate-ovate, inequilateral, equivalve, moderately inflated; umbo broad, not so prominent, located at about two fifths of the length; antero-dorsal margin nearly straight, gradually bending down rounded anterior portion; postero-dorsal margin long, broadly concave, abruptly turned to posterior margin at rostrated posterior end; ventral margin smoothly convex; lunule indistinct; escutcheon broadly concave, circumscribed by a blunt ridge from beak to posterior end; external surface sculpted all over with densely spaced distinct commarginal ribs; anterior teeth about 11 in number, posterior teeth more than 10; muscle scar and pallial line unknown.

Comparison.—This new species is most similar to *Neilonella soyoe* Habe, 1958, a Japanese living species, in shell size and form. However, *N. soyoe* is distinguished from this new species by its smoother surface. *Neilonella isensis* Shibata, 1970 differs from this new species in its smaller shell size and higher shell outline with coarser commarginal ribs.

Judging from descriptions, this new species may be conspecific with *Neilonella* cf. *soyoe* of Shibata in Itoigawa et al. (1974) and Itoigawa et al. (1981, 1982) from the Oidawara Formation in Gifu Prefecture. It is, however, difficult to conclude that the two forms are conspecific because these authors illustrated only a poorly preserved internal mold.

Measurements.—Holotype, Length 7.9 mm, height 4.6 mm,

width 2.4 mm [Figure 5-8; IGUT 1184-1]. Paratypes, length 9.2 mm, height 4.8 mm, width 2.2 mm [Figure 5-9; IGUT 11834-2]; length 8.1 mm, height 4.6 mm, width 2.0 mm [Figure 5-10; IGUT 11834-3].

Family Cuspidariidae

Genus *Myonera* Dall, 1886

Myonera osawanoensis (Tsuda, 1959)

Figures 6-25, 26, 27

Cuspidaria osawanoensis Tsuda, 1959, p. 73, pl. 2, figs. 2a, b.

Cuspidaria sp. Shibata in Itoigawa et al., 1974, p. 110, pl. 35, figs. 3, 4.

Cuspidaria (*Tergula*) sp. Itoigawa et al., 1981, pl. 22, fig. 9; Itoigawa et al., 1982, p. 119.

Remarks.—Many specimens referred to this species were obtained from Locs. 1 and 2, but most of them were damaged during the sampling. This species is characterized by having a well inflated disc with rough commarginal undulations and a depressed and triangle-shaped rostrum. The shell outline is somewhat variable in the examined specimens as illustrated.

This species is closely related to *Myonera dautzenbergi* Prasad, 1932, which currently inhabits bathyal depths in Sagami Bay and Indonesian waters (Higo and Goto, 1993), but differs in surface ornamentation. The external surface of the disc of *M. dautzenbergi* is not sculptured with rough undulations.

This species was originally described by Tsuda (1959) under the genus *Cuspidaria* from the Miocene Kurosedani Formation in Toyama Prefecture, but is treated herein as a *Myonera* by virtue of having an umbonal-ventral sharp step separating the rostrum from the disc, which is a diagnostic character of *Myonera*.

Judging from their description and illustration, *Cuspidaria* sp. (n. sp.) of Shibata in Itoigawa et al. (1974) and *Cuspidaria* (*Tergula*) sp. of Itoigawa et al. (1981, 1982) from the Oidawara Formation in Gifu Prefecture seem to be included within the variation of this species.

Measurements.—Length 11.0 mm, height 6.9 mm, width 2.4 mm [Figure 5-25; IGUT 11845-3]; length 9.5 mm, height 7.1 mm [Figure 5-26; IGUT 11845-2]; length 9.0 mm, height 7.0 mm, width 2.4 mm [Figure 5-27; IGUT 11845-1].

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Apparatus of a Triassic conodont species *Cratognathodus multihamatus* (Huckriede)

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Abstract. A Triassic conodont *Cratognathodus multihamatus* (Huckriede) from the pelagic limestone of the Taho Formation in Ehime Prefecture, Southwest Japan is newly reconstructed as an octomembrate apparatus with segminate Pa, angulate Pb, breviform digyrate M, alate Sa, breviform digyrate Sb₁, extensiform digyrate Sb₂, bifurcate bipennate Sc₁, and bipennate Sc₂ elements. Among the elements, the Pb, M, and S series were regarded as those of a septimembrate or octomembrate species *Gladigondolella tethydis* (Huckriede) by previous authors. *Cr. multihamatus* may comprise a lineage of the Gondolellidae; it occurs in the Tethyan realm and ranges from late Spathian or early Anisian to late Carnian.

Key words: *Cratognathodus multihamatus* (Huckriede), Gondolellidae, octomembrate apparatus, Taho Formation, Triassic

Introduction

The form species of conodonts, *Cratognathodus kochi* (Huckriede, 1958), *Cratognathodus posterognathodus* Mosher 1968, *Cypridodella venusta* (Huckriede, 1958), *Diplododella lautissima* (Huckriede, 1958), *Enantiognathus stoppeli* (Bender, 1967), *Cypridodella spengleri* (Huckriede, 1958), *Hindeodella petrae-viridis* Huckriede 1958, and *Hindeodella multihamata* Huckriede 1958 were recovered from the Triassic in various areas of Tethyan realm. These eight form species also occur abundantly in the limestone strata of the Taho Formation outcropped at Tahokamigumi, Shirokawa-cho, Higashi-ura-gun, Ehime Prefecture in Shikoku. As a result of statistic analysis of conodont fauna with these form species from various levels of the upper Spathian or lower Anisian to middle Anisian and upper Carnian strata of the formation, it has been made clear that these form species are the elements of a conodont skeletal apparatus and *Cr. kochi*, *Cr. posterognathodus*, *Cy. venusta*, *D. lautissima*, *E. stoppeli*, *Cy. spengleri*, *H. petrae-viridis*, and *H. multihamata* are assigned to the Pa, Pb, M, Sa, Sb₁, Sb₂, Sc₁, and Sc₂ elements, respectively.

I propose *Cratognathodus multihamatus* (Huckriede) herein for this octomembrate apparatus and describe the elements of the apparatus. Furthermore, I scrutinize the phylogeny of this species and compare it with the previously reconstructed Triassic and some Paleozoic conodont apparatuses.

All of the described specimens are kept in the Department of Science Education, Faculty of Education and Human

Sciences, Yokohama National University (YNU).

Biostratigraphic setting

The limestone strata of the Taho Formation attain approximately 75 m in thickness and correspond to Griesbachian to middle Anisian and upper Carnian to lower Norian. Upper Anisian to lower Carnian strata are missing due to a fault (Koike, 1996).

In the Taho Formation, *Cratognathodus multihamatus* ranges from the uppermost part of the *Neospathodus homeri* Zone in the upper Spathian or the basal part of the *Chiosella timorensis* Zone in the lower Anisian to the *Metapolygnathus nodosus* Zone in the upper Carnian. The elements of this species are particularly abundant in the lower Anisian where 930 specimens were recovered from approximately 5 kg of limestone from level 1197. On the other hand, they are very rare in number and poor in preservation in the upper Carnian (Table 1).

Cratognathodus multihamatus is a Tethyan species and the elements of the species were reported as form species from various parts of the Tethyan realm by many authors. In the biostratigraphic study of conodonts in Austria, Huckriede (1958) proposed and described the form species *Prioniodina kochi*, *Lonchodina venusta*, *Roundya lautissima*, *Lonchodina spengleri*, *Hindeodella petrae-viridis*, and *Hindeodella multihamata*. These species are assigned to the Pa, M, Sa, Sb₂, Sc₁, and Sc₂ elements of the *Cr. multihamatus* apparatus, respectively. The form species *Ozarkodina saginata* de-

Table 1. Occurrence of Pa, Pb, M, Sa, Sb₁, Sb₂, Sc₁, and Sc₂ elements of *Cratognathodus multihamatus* (Huckriede) obtained from 3 to 5 kg of limestone of the Tahoe Formation.

| Stratigraphic level | Elements | | | | | | | | |
|---------------------|----------|-----|-----|-----|-----------------|-----------------|-----------------|-----------------|---------------------------------------|
| | Pa | Pb | M | Sa | Sb ₁ | Sb ₂ | Sc ₁ | Sc ₂ | Sc ₁ ? + Sc ₂ ? |
| Carnian | | | | | | | | | |
| 1133 | 13 | 10 | 3 | 2 | 1 | 2 | 5 | 1 | 3 |
| Anisian | | | | | | | | | |
| 1202 | 31 | 50 | 49 | 9 | 27 | 13 | 11 | 20 | 51 |
| 1199 | 14 | 9 | 9 | 2 | 9 | 8 | 2 | 2 | 4 |
| 1198 | 29 | 20 | 8 | 5 | 3 | 4 | 4 | 9 | 8 |
| 1197 | 242 | 126 | 150 | 18 | 82 | 51 | 19 | 164 | 79 |
| 1196 | 20 | 6 | 9 | 3 | 6 | 14 | 3 | 12 | 12 |
| 1195 | 38 | 18 | 28 | 6 | 8 | 9 | 6 | 29 | 13 |
| 1324 | 23 | 5 | 6 | 3 | 4 | 4 | 1 | 4 | 7 |
| 1132 | 18 | 5 | 14 | 2 | 10 | 11 | 10 | 10 | 8 |
| 1194 | 52 | 13 | 26 | 5 | 10 | 12 | 8 | 18 | 11 |
| 1323 | 63 | 31 | 35 | 3 | 17 | 29 | 7 | 30 | 15 |
| 016 | 29 | 28 | 21 | 8 | 9 | 31 | 8 | 50 | 19 |
| 1193 | 143 | 45 | 38 | 12 | 33 | 36 | 17 | 54 | 39 |
| 1130 | 74 | 40 | 17 | 5 | 21 | 27 | 10 | 29 | 30 |
| 1322 | 70 | 32 | 25 | 6 | 18 | 25 | 8 | 17 | 36 |
| 1129 | 95 | 32 | 45 | 17 | 34 | 49 | 13 | 27 | 38 |
| 1321 | 155 | 67 | 68 | 15 | 43 | 65 | 19 | 55 | 29 |
| 015 | 45 | 14 | 7 | 3 | 12 | 13 | 2 | 29 | 13 |
| 1192 | 12 | 9 | 11 | 2 | 6 | 3 | 4 | 9 | 7 |
| 1128 | 34 | 16 | 16 | 3 | 7 | 9 | 4 | 10 | 16 |
| 014 | 37 | 19 | 14 | 2 | 3 | 12 | 3 | 14 | 9 |
| 1191 | 59 | 48 | 50 | 16 | 29 | 37 | 11 | 18 | 19 |
| 1127 | 265 | 113 | 135 | 39 | 72 | 113 | 48 | 63 | 86 |
| 1316 | 66 | 35 | 32 | 7 | 23 | 19 | 9 | 22 | 17 |
| Spathian ? | | | | | | | | | |
| 013 | 42 | 26 | 26 | 9 | 7 | 11 | 3 | 19 | 12 |
| 1183 | 18 | 3 | 6 | 1 | 2 | 8 | 2 | 6 | 2 |
| total | 1687 | 821 | 845 | 203 | 615 | 495 | 237 | 721 | 583 |
| ratio | 8.3 | 4.0 | 4.2 | 1 | 3.0 | 2.4 | 1.2+ | 3.6+ | |

scribed by Huckriede (1958) was distinguished from the form species *Cratognathodus posterognathus* Mosher (Pb element of *Cr. multihamatus* apparatus) by its shorter posterior process (Mosher, 1968). The form species *Ozarkodina saginata* illustrated by Huckriede (1958) is, however, probably based on incomplete specimens of *Cr. posterognathus* lacking a part of the posterior process. The specimen of the form species *Apatognathus* sp. illustrated by Huckriede (1958) is poorly preserved but the features of the processes and denticulation agree well with those of the Sb₁ element of *Cr. multihamatus*. According to Huckriede (1958), most of the form species occur commonly in the upper Anisian to Carnian.

Bender (1967) reported Spathian and early Anisian conodonts from Chios and other Greek islands in the Mediterranean Sea and described the Pa, Pb, M, Sb₂, Sc₁, and Sc₂ elements of *Cr. multihamatus* as the form species proposed by Huckriede (1958). The specimens of the form species *Hindeodella stoppeli* illustrated by Bender (1967) are incomplete but the features of the lateral processes agree with the Sb₁ element of *Cr. multihamatus*. The Pa and Pb elements occur first in the upper part of the middle

Neospathodus homeri Zone (late Spathian or early Anisian) and other elements occur first in the lower or middle part of the lower *N. homeri* Zone (late Spathian).

Mosher (1968) studied Triassic conodonts of Austria, North America, and Germany, and described the form species assignable to the Pa, Pb, M, Sa, Sb₂, Sc₁, and Sc₂ elements of *Cr. multihamatus* from the Middle and Upper Triassic limestones in Austria. In part the specimens illustrated as the form species *Prioniodina petrae-viridis* by Mosher (1968, Pl. 116, Figs. 30, 31) are referable to the Sb₁ element. Furthermore, Mosher (1968) reported the occurrence of the Pb, Sb₁, and Sc₂ ? elements in the Middle and Upper Triassic of North America, but did not report any occurrences of the elements of *Cr. multihamatus* in the Muschelkalk of Germany. According to Mosher (1968), all of the elements appear first in the late Anisian and the Pb, M, Sa, and Sc₁ elements range to early Ladinian, but the Pa, Sb₁, Sb₂, and Sc₂ elements range to Carnian or Norian in Austria.

In their biostratigraphic study of the Lower to Upper Triassic conodonts in some areas of Europe in the Tethyan

realm, Kozur and Mostler (1972) described the form species referable to the Pb, M, Sa, and Sb₂ elements of *Cr. multihamatus*. One of the specimens of the form species *Hindeodella spengleri* (Huckriede) illustrated by Kozur and Mostler (1972, pl. 7, fig. 11) is referable to the Sc₁ element of *Cr. multihamatus*. Most of the specimens of the form species *Enantiognathus petraeviridis* (Huckriede) illustrated by Kozur and Mostler (1972, pl. 10, figs. 1, 2; pl. 14, figs. 4, 5, 8, 12) are the Sb₁ element of *Cr. multihamatus*. The form species *Cratognathodus kochi*, the Pa element of *Cr. multihamatus*, is regarded as the immature form of the "gladigondolelliform" (Pa) element of *Gladigondolella tethydis* (Huckriede) by Kozur and Mostler (1972). According to them, the biostratigraphic ranges of the elements are within the Ladinian to early Carnian.

In the report on Triassic conodonts from Turkey, Gedik (1975) described the form species referable to the Pa, Pb, M, Sb₂, and Sc₂ elements of *Cr. multihamatus*. The specimens illustrated by Gedik (1975) as the form species *Hibbardella magnidentata* (Tatge) (pl. 4, figs. 8-10), *Enantiognathus ziegleri* (Diebel) (pl. 5, fig. 3), and *Prioniodina (Frabellignathus) latidentata* (Tatge) (pl. 8, figs. 13-15) are probably referable to the Sa, Sb₁, and Sc₁ elements of *Cr. multihamatus*, respectively. According to Gedik (1975), all of the elements appear first in the Zone A of the early Anisian just above the *Chiosella timorensis* Zone and range to the late Carnian.

Summarizing the above-mentioned reports, *Cr. multihamatus* is a diagnostic species in the Tethyan realm and ranges from late Spathian or early Anisian to late Carnian as recognized in the Tahoe Formation.

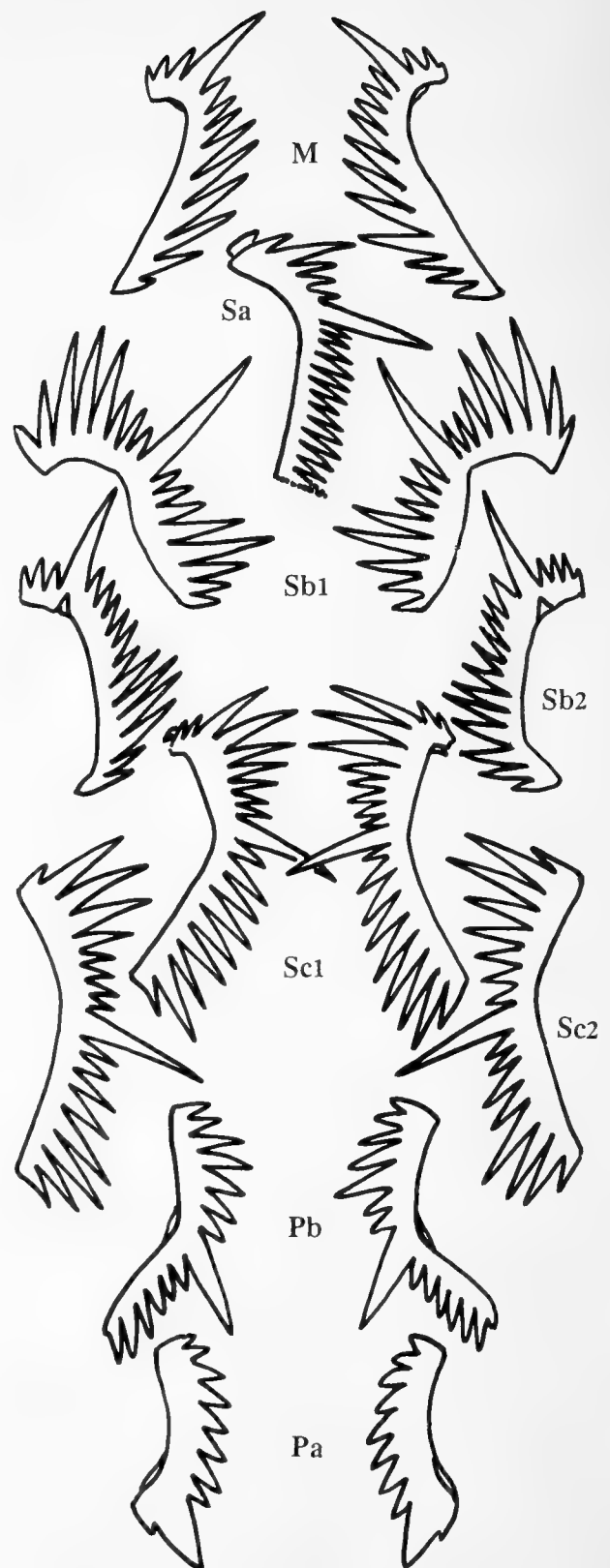
Apparatus of *Cratognathodus multihamatus* (Huckriede)

Cratognathodus multihamatus is reconstructed as an octomebrate skeletal apparatus in this study (Figure 1). The elements are Pa, Pb, M, Sa, Sb₁, Sb₂, Sc₁, and Sc₂.

The Pa element is a segminate (neospathodiform) type having an arched anterior process with 3 to 10 relatively short and broad, discrete denticles, a large broad cusp, and an expanded basal cavity. One or two small denticles may be present behind the cusp. It is identical with the form species *Cratognathodus kochi* (Huckriede, 1958).

The Pb element is an angulate (ozarkodiniform) type possessing a strongly and laterally bending unit, an anterior process with 3 to 6 relatively large, discrete denticles, a posterior process with 4 to 6 short, slender, discrete denticles, a large cusp, and a slightly expanded basal cavity. It is identical with the form species *Cratognathodus saginatus* (Huckriede, 1958) and *Cratognathodus posterognathus* Mosher, 1968.

The M element is a breviform digyrate (cypridodelliform) type having a short lateral process with 1 to 3 short denticles, a long lateral process with 8 to 10 short to long denticles, a large cusp, and an expanded basal cavity. It is identical



→ **Figure 1.** A hypothetically reconstructed apparatus of *Cratognathodus multihamatus* (Huckriede) from the Tahoe Formation.

with the form species *Cypridodella venusta* (Huckriede, 1958).

The Sa element is an alate (diplododelliform) type possessing 2 long lateral processes with 3 to 5 short to long, discrete denticles, a long posterior process with more than 10 short, indiscrete denticles, a large cusp, and a slightly expanded basal cavity. It is identical with the form species *Diplododella lautissima* (Huckriede, 1958).

The Sb₁ element is a breviform digyrate (enantiognathiform) type possessing subequal-sized slender lateral processes with 7 to 10 short to long, discrete denticles, a slender long cusp, and a slitlike basal cavity. It is probably identical with the form species *Enantiognathus stoppeli* (Bender, 1967).

The Sb₂ element is an extensiform digyrate (prioniodiniform) type having a short lateral process with 2 to 5 short denticles, a long lateral process with 10 to 13 short to long, indiscrete denticles, a slender long cusp, and a triangular basal cavity. It is identical with the form species *Cypridodella spengleri* (Huckriede, 1958).

The Sc₁ element is a bipennate (hindeodelliform) type possessing a bifurcate long anterior process with 5 to 8 short to long, discrete denticles, a long posterior process with more than 5 short to long, discrete denticles, a slender long cusp, and a slitlike basal cavity. It is identical with the form species *Hindeodella petrae-viridis* Huckriede, 1958.

The Sc₂ element is a bipennate (hindeodelliform) type having slender long anterior and posterior processes carrying 5 to 12 short to long, discrete denticles, a slender long cusp, and a slitlike basal cavity. It is identical with *Hindeodella multihamata* Huckriede, 1958.

The number of elements of *Cr. multihamatus* occurring in each level is shown in Table 1. The frequencies of the Pa, Pb, M, Sa, Sb₁, Sb₂, Sc₁, and Sc₂ elements from the samples of the Spathian or Anisian to Carnian are 1687, 812, 845, 203, 615, 495, 237+, and 721+, and an approximate ratio of the elements is 8.3:4.0:4.2:1:3.0:2.4:1.2+:3.6+, respectively.

The natural assemblage of *Neogondolella* sp. recovered by Rieber (1980) from the Middle Triassic of Switzerland and *Gondolella pohli* reconstructed by von Bitter and Merrill (1998) based on many natural assemblages from Illinois are composed of a single unpaired alate Sa, single pairs of segminiplanate Pa, angulate Pb, breviform digyrate M, breviform digyrate Sb₁, and extensiform digyrate Sb₂, and two pairs of bipennate Sc elements. Orchard (1998) regarded, however, the Sc elements in *Neogondolella* as being composed of Sc₁ and Sc₂, and the *Neogondolella* apparatus as an octomembrate type.

As mentioned further on, *Cr. multihamatus* represents a close phylogenetic relationship with neogondolellids and is referable to the Gondolellidae. Therefore, *Cr. multihamatus* probably has as many elements as *Neogondolella* sp. (Rieber, 1980) and *G. pohli*. In that case, the abundance of segminiplanate Pa elements is very high compared with other elements in *Cr. multihamatus*. The reason is probably due to robustness of Pa elements. On the other hand, alate Sa elements are considerably low in abundance. This is presumably due to their fragility. The same tendency in abundance of Pa and Sa elements is observed in apparatuses of *G. pohli* (von Bitter and Merrill, 1998, table 1).

***Cratognathodus multihamatus* and previously reconstructed apparatuses**

Kozur and Mostler (1971) reconstructed a multielement species *Gladigondolella tethydis* (Huckriede) with 11 or 12 elements. The elements are identical with the form species *Cr. posterognathus*, *Cy. venusta*, *D. lautissima*, *Cy. spengleri*, *H. petrae-viridis*, *H. multihamata*, *Cr. saginatus*, *Didymodella alternata* (Mosher), *Lonchodina hungarica* Kozur and Mostler, *H. pectiniformis* (Huckriede), and *G. tethydis*. Among these form species, the first six correspond with the Pb, M, Sa, Sb₂, Sc₁, and Sc₂ elements of the *Cr. multihamatus* apparatus, respectively. Furthermore, one of the specimens demonstrated as *Enantiognathus petraeviridis* by Kozur and Mostler (1971, pl. 1, fig. 14) is referable to the Sb₂ element of *Cr. multihamatus*.

Hirsch (1981, 1994) also reported a multielement species *G. tethydis* composed of eight elements. Judging from the simple illustration by Hirsch (1994), the eight elements are identical with the form species, *Cr. posterognathus*, *Cy. venusta*, *D. lautissima*, *H. petrae-viridis*, *H. multihamata*, *Cr. saginatus*, *H. pectiniformis*, and *G. tethydis*. As mentioned above, the first five form species correspond with the Pb, M, Sa, Sc₁, and Sc₂ elements of *Cr. multihamatus*, respectively.

The correlation coefficient of occurrence is very low between the *Cr. multihamatus* apparatus and the Pa element of *G. tethydis* in the Tahoe Formation: *Cr. multihamatus* appears first at the upper part of the *Neospathodus homeri* Zone in the late Spathian or the basal part of the *Cr. timorensis* Zone in the early Anisian but the Pa element of *G. tethydis* appears later, at the base of the *Paragondolella bulgarica* Zone (Figure 2). Among the studied samples yielding *Cr. multihamatus* (Table 1), the occurrence of the Pa elements of *G. tethydis* is restricted within the levels 1197, 1198, and 1202 in the *P. bulgarica* Zone and the number of the elements found in about 3 to 5 kg of limestone is only 2, 2, and 25, respectively.

According to Muttoni *et al.* (1998), the Pa elements of *G. tethydis* appear first near the base of the *Paragondolella bifurcata*-*Neospathodus kockeli* Zone in Pelsonian of Anisian of Italy. The first appearance of the Pa elements of *G. tethydis* in Italy is nearly the same in age as their first appearance in Japan. As mentioned previously, *Cr. multihamatus* appears first in the late Spathian or earliest Anisian in Tethyan realm. Therefore, the first appearances of *Cr. multihamatus* and the Pa element of *G. tethydis* are obviously different in the Tethyan realm.

Kozur and Mostler (1972) regarded the form species *Cr. kochi* (=Pa elements of *Cr. multihamatus*) as immature forms of the "gladigondolelliform" (Pa) elements of *G. tethydis*. As mentioned above, mature forms of the Pa elements of *G. tethydis*, however, never occur in the *N. homeri* and *Cr. timorensis* Zones which yield the abundant form species *Cr. kochi*. Furthermore, Pa elements of *Cr. multihamatus* and immature forms of Pa elements of *G. tethydis* are easily distinguished from each other by the feature of lateral expansion of process, denticulation, and the shape of the basal cavity.

As far as observed conodont faunas in Japan are con-

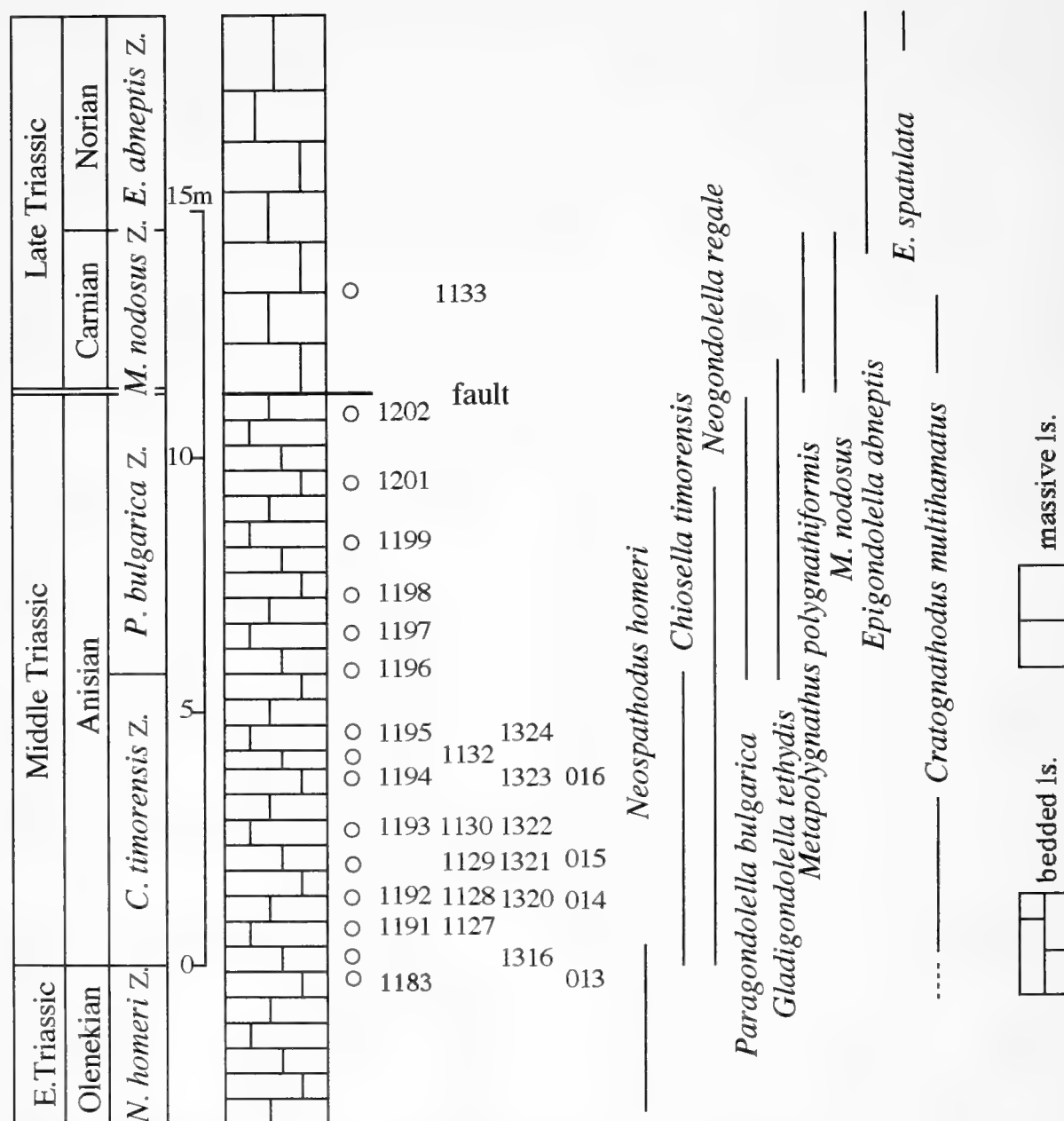


Figure 2. Stratigraphic section and vertical distribution of *Cratognathodus multihamatus* (Huckriede) and important pectiniform conodonts in the Taho Formation.

cerned, the correlation coefficient of occurrence is very low among the Pa element of *G. tethydis* and other pectiniform and ramiform elements. For example, a late Anisian or early Ladinian limestone sample collected from Izuriha near Kyoto yields about 550 specimens of *G. tethydis* Pa elements, but other elements associated with them are mainly of the *Cr. multihamatus* apparatus with some "ozarkodiniiform" Pb and a few "enantiognathiform" Sb₁ of unidentified apparatuses. The abundances of the Pa, Pb, M, Sa, Sb₁, Sb₂, Sc₁, and Sc₂ elements of *Cr. multihamatus* in the sample are 19, 56, 36, 17, 30, 59, 72+, and 33+, respectively. Thus, the *G.*

tethydis apparatus reconstructed by Kozur and Mostler (1971) and Hirsch (1981, 1994) is problematical. Furthermore, it is difficult to reconstruct *G. tethydis* as a multielement apparatus with Pa and any other elements at present.

Phylogeny of *Cratognathodus multihamatus*

As mentioned above, *Cr. multihamatus* is characterized by possessing segminate Pa, angulate Pb, breviform digyrate M, alate Sa, breviform digyrate Sb₁, extensiform digyrate Sb₂, bifurcate bipennate Sc₁, and bipennate Sc₂ elements.

Among these elements, Pa is one of the most important components for scrutinizing the phylogeny of *Cr. multihamatus*.

The Pa element of *Cr. multihamatus* with a relatively large cusp and large discrete denticles is morphologically very different from not only the typical Spathian neospathodid species: *Neospathodus homeri* (Bender) and *N. triangularis* (Bender) but also from the immature forms of the typical Anisian neogondolellid, paragondolellid, and chiosellid species: *Neogondolella regale* Mosher, *Paragondolella bulgarica* (Budurov and Stefanov), and *Chiosella timorensis* (Nogami), all of which exhibit a small cusp and subequal indiscrete denticles. The Pa element of *Cr. multihamatus*, however, represents some morphologic similarities to the immature forms of the Pa elements of *Gladigondolella tethydis*, which appeared later than *Cr. multihamatus* in Anisian time, and *Paragondolella navicula* (Huckriede) and *P. hallstattensis* Mosher, which appeared in Norian time. Furthermore, the Pa element closely resembles the "ozarkodiniform" element of *Celsigondolella watznaueri watznaueri* (Kozur) and the form species *Pollognathus sequens* (Kozur), which are regarded as the endemic Ladinian conodont species of the German Basin (Kozur and Mostler, 1972; Kozur, 1989).

The presence of "enantiognathiform" Sb₁ element in *Cr. multihamatus* is also considerably important in establishing its phylogenetic relationship with the previously reconstructed conodonts. The natural assemblage of *Neogondolella* sp. recovered by Rieber (1980) from the Middle Triassic of Switzerland is composed of as many as 15 elements belonging to Pa, Pb, M, Sa, Sb₁, Sb₂, and Sc (von Bitter and Merrill, 1998). The Sb₂ element of *Neogondolella* sp. is of the typical "enantiognathiform" type (von Bitter and Merrill, 1998) and morphologically quite similar to the Sb₁ of *Cr. multihamatus*. The Pennsylvanian *Gondolella pohli* reconstructed by von Bitter and Merrill (1998) based on natural assemblages from Illinois also includes a single pair of "enantiognathiform" Sb₂ elements accompanied by a single unpaired Sa, single pairs of Pa, Pb, M, and Sb₁, and two pairs of Sc elements.

Orchard (1998) reviewed all gondolellids and pointed out that *Neogondolella* is an octomembrate apparatus with an "enantiognathiform" type occupying the Sb₁ position adjacent to the Sa element and a single pair of Sc elements always having a bifurcate anterior process. Orchard (1998) regarded the Sc element with a bifurcate anterior process as the Sc₂ but now is of the opinion that it is the Sc₁ (personal communication).

In addition to the "enantiognathiform" element, the presence of the Sc element with a bifurcate anterior process in *Cr. multihamatus* represents a phylogenetic relationship with *Neogondolella*. Furthermore, the Pb, M, Sa, and Sb₁ elements of *Cr. multihamatus* also basically have the same morphology as those of *Neogondolella* sp. and *Gondolella pohli*.

The skeletal apparatus of *Pseudofurnishius murcianus* reconstructed by Ramovš (1977, 1978) based on many clusters in the upper Ladinian of Slovenia is setpimembrate with "enantiognathiform" elements. The "pollognathiform" element of *P. murcianus* shows some similarities to the Pa

elements of *Cr. multihamatus*. The "pollognathiform" elements were identified with *Pollognathus sequence* by Ramovš (1977). All elements except for the "pseudofurnishiform" Pa and "chirodelliform" Sb₁? elements in *P. murcianus* are basically similar to their counterparts in *Cr. multihamatus*.

The Ladinian *Budurovignathus mungoensis* (Diebel) apparatus reconstructed by Mietto (1982) based on clusters from Italy also includes "enantiognathiform" elements with the Pa, M, Sa, and Sc elements.

The *Xaniognathus* and *Cypridodella* apparatuses statistically reconstructed by Sweet (1981, 1988) are composed of six elements such as the Pa, Pb, M, Sa, Sb, and Sc, among which the Pb is regarded as the "enantiognathiform" digyrate type. The Pb element is closely similar to the Sb₂ element of *Neogondolella* sp. of Rieber (1980). Sweet (1988) regarded *Neogondolella*, *Gondolella*, *Xaniognathus*, and *Cypridodella* as belonging to the family Gondolellidae based on the common occurrence of "enantiognathiform" elements among their apparatuses, and as having a close phylogenetic relationship with *Ellisonia* of the family Ellisoniidae, which also bears "enantiognathiform" elements. *Pseudofurnishius* and *Budurovignathus* are as well included in the Gondolellidae by many authors (Sweet, 1988; Kozur, 1989, and others).

Although Dzik (1991) recognized that *Gondolella* is characterized by the presence of lo (enantiognathiform) elements, he claimed the presence of enantiognathiform-like elements in some undescribed apparatuses of the Devonian Hibbardellidae which are unlikely to have any relationships to *Gondolella*.

Sweet (1988) assumed the origin of both of the Gondolellidae and Ellisonidae to be *Idioproniodus* or a closely related genus with "enantiognathiform" elements in the Mississippian. Von Bitter and Merrill (1998) also considered that the Mississippian *Idioproniodus* is a likely ancestor of the Pennsylvanian *Gondolella* based on their recognition of an evolutionary trend of reduction of the posterior process in the anguliplanate Pa elements.

Dzik (1991) pointed out that reduced posterior processes in the platform (p) elements are characteristic of *Gondolella* and a similar feature occurs in some Devonian *Ozarkodina*. On the basis of morphologic similarities in both platform and ramiform elements. Dzik (1991) regarded the Devonian *Pinacognathus* (?) sp. as the probable ancestor of the Gondolellidae.

In summary, I conclude that *Cr. multihamatus* should be included in the Gondolellidae because *Cr. multihamatus* has segminate Pa elements similar to immature forms of some neogondolellid Pa elements and bears "enantiognathiform" Sb₁ elements which are common in the Gondolellidae, and Sc₁ and other elements which are basically similar in morphology to those of neogondolellid and gondolellid apparatuses.

The segminate Pa elements in *Cr. multihamatus* represent close morphologic similarity with the anterior process of the angulate (ozarkodiniform) Pb elements, which are basically the same in morphology as those of *Neogondolella* sp. of Rieber (1980) and *Gondolella pohli*. This feature suggests

that both elements in the P position have a mutual relationship in feeding mechanism, but while the Pa elements acquired broad variation in morphology (anguliplanate *Gladigondolella*, segminate *Neospathodus*, and segminiplanate *Gondolella* and *Neogondolella*), the Pb element remained angulate during the evolution of the Gondolellidae. The ancestral form of the Pa elements of the Gondolellidae may be referable to an angulate (ozarkodiniform) element like the Pb elements.

In that case the ancestor of the Gondolellidae should be searched for in conodonts with "ozarkodiniform"-like Pa and "ozarkodiniform" Pb elements. The conodonts possessing such Pa and Pb elements were not included in the Ordovician family-group of the order Prioniodinida Sweet, 1988 in which the family Gondolellidae was included by Sweet (1988). On the other hand, Ordovician conodonts *Bryantodina? staufferi* Bergström and Sweet and *Plectodina* of Sweet (1988) in the Spathognathodontidae of the order Ozarkodinida Dzik, 1976 possess "ozarkodiniform"-like Pa and "ozarkodiniform" Pb elements (Sweet, 1988).

Dzik (1991) included the order Prioniodinida erected by Sweet (1988) within the order Ozarkodinida and regarded the Gondolellidae as having a phylogenetic relationship with the Spathognathodontidae.

On the basis of morphologic similarity between the Pa and Pb elements in *Cr. multihamatus* and those of the species in the Spathognathodontidae, I would like to support the opinion of Dzik (1991) that the Gondolellidae is phylogenetically related to the Spathognathodontidae of the order Ozarkodinida.

Systematic Paleontology

Phylum Conodonta
Order Ozarkodina
Superfamily Gondolellacea
Family Gondolellidae
Genus *Cratognathodus*

Type species.—*Hindeodella multihamata* Huckriede, 1958, p. 148–149.

Revised diagnosis.—*Cratognathodus* newly proposed herein contains species with octomembrate apparatus of as many as 15 elements: single pairs of segminate Pa, angulate Pb, breviform digyrate Sb₁, extensiform digyrate Sb₂, bipennate Sc₁ and Sc₂ elements, and a single unpaired alate Sa element. Pa elements characterized by relatively broad cusp with expanded basal cavity and large discrete denticles.

Remarks.—Mosher (1968) enacted the genus *Cratognathodus* and included the following four form species in the genus, *Prioniodina kochi* Huckriede, *Cr. posterognathus* newly proposed, and two unidentified species, which are both characterized by the presence of a strong broad cusp with a widely expanded basal cavity, and relatively small number of discrete denticles. As mentioned previously, *Cratognathodus kochi* and *Cr. posterognathus* are respectively identical with the Pa and Pb elements of the *Cr. multihamatus* apparatus. Among the three specimens illustrated as *Cr. kochi* by Mosher (1968), one specimen (pl. 113, fig. 7) is misidentified and another specimen (pl. 113, fig. 4) is not a typical Pa element of the *Cr. multihamatus* apparatus. Mosher (1968), however, regarded the form species *Prioniodina kochi* Huckriede as the type species of his *Cratognathodus*.

Later, Kozur and Mostler (1972) claimed that the genus *Cratognathodus* created by Mosher (1968) is not a valid taxon because the holotype and all other specimens previously described as the form species *Cr. kochi* are immature forms of the "gladigondolelliform" (Pa) elements of *Gladigondolella tethydis* (Huckriede).

Based on my observation on Pa elements of *G. tethydis* from the Taho Formation and other limestone formations in Japan, the immature forms of the element are characterized by a narrow platform-like anterior process and gradually increasing denticles in length toward the anterior as observed in the mature forms. The immature forms of the Pa elements of *G. tethydis* can be, therefore, easily distinguished from the form species *Cr. kochi* (= Pa element of *Cr. multihamatus*).

The Pa element of *Cr. multihamatus* represents various features in the shape and size of the cusp and denticulation on the anterior process (Figure 3). The holotype of the form species *Cr. kochi* (Huckriede, 1958, pl. 12, fig. 11) possessing a short broad cusp and subequal denticles is safely assigned within the range of morphologic variation of the Pa element of *Cr. multihamatus* and agrees well with the specimens illustrated in Figure 3–16, 26.

Cratognathodus multihamatus (Huckriede)

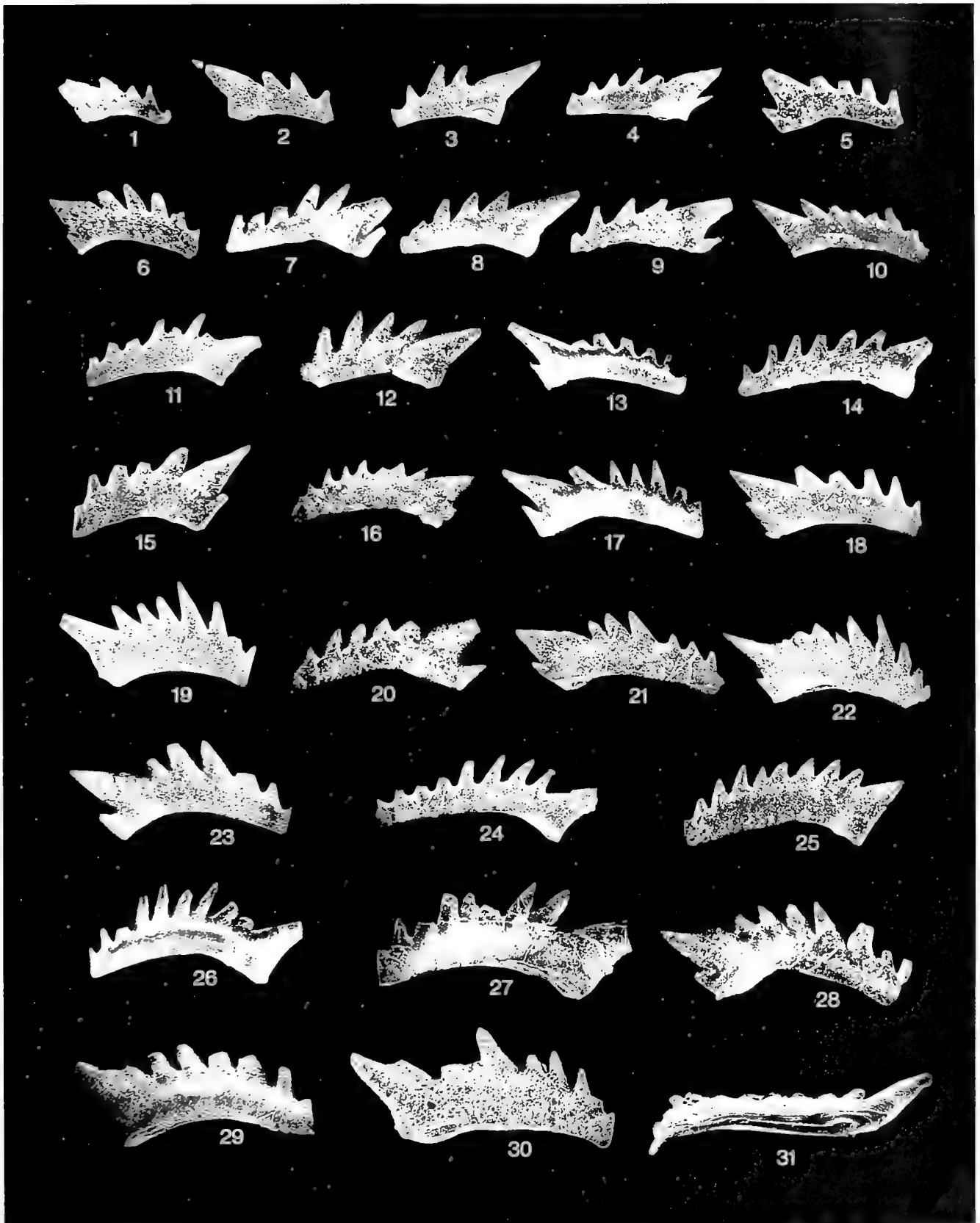
Figures 3–5

Pa element

Prioniodina kochi Huckriede, 1958, p. 159, pl. 11, fig. ?37, pl. 12, figs. 11, 12, pl. 14, fig. 4; Spasov and Ganey, 1960, p. 89, pl. 1, fig. 23, pl. 2, fig. 12; Catalov and Stefanov, 1966, pl. 1, fig. 3; Bender, 1967, p. 527, non pl. 5, fig. 12; Hirsch, 1969, pl. 1, fig. ?7.

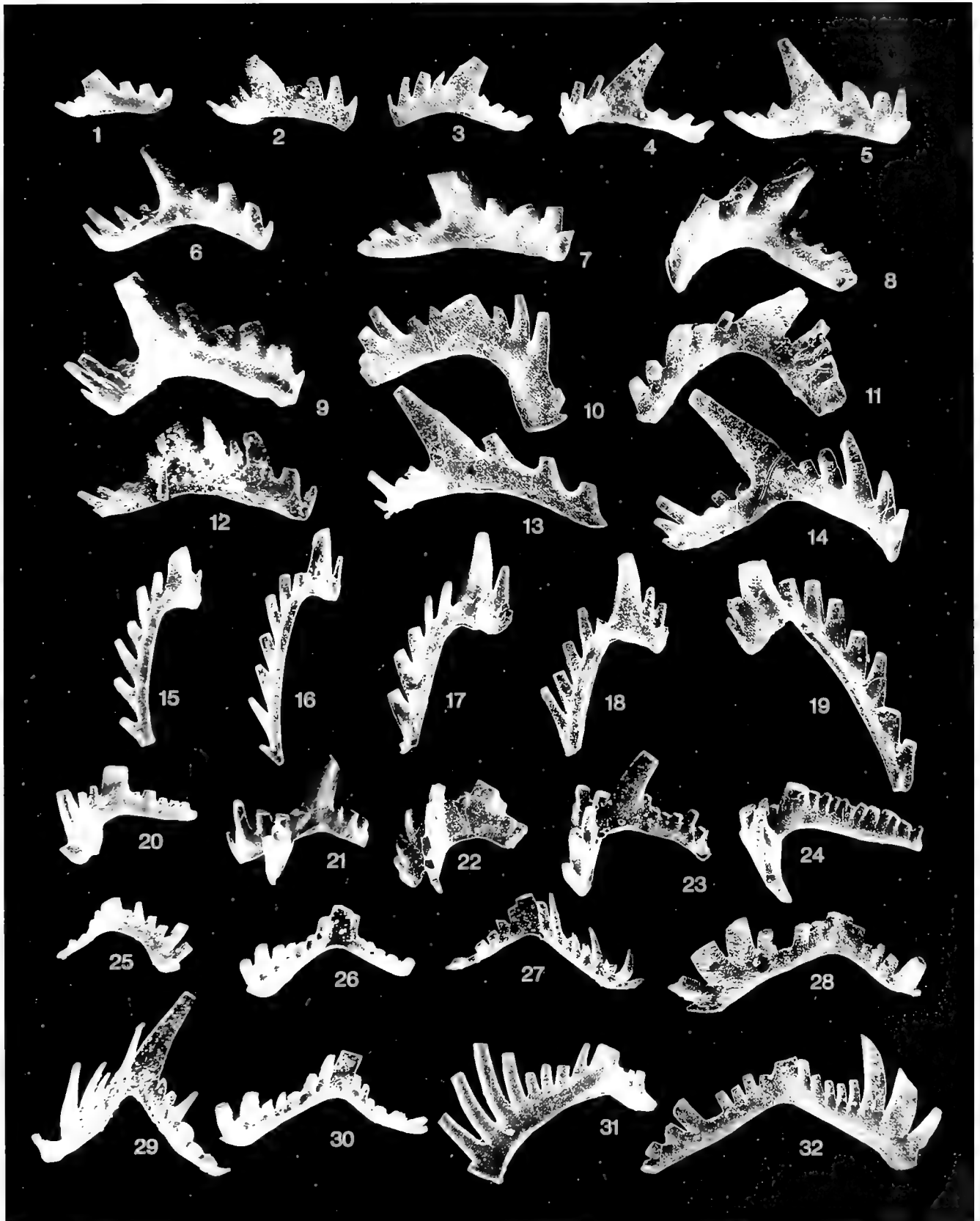
Neoprioniodus cf. kochi (Huckriede), Ishii and Nogami, 1966, non

→ **Figure 3.** 1–31, Pa elements of *Cratognathodus multihamatus* (Huckriede) from the Taho Formation, all ×60. 1: YNUC15881 from Lev. 1316. 2: YNUC15882 from Lev. 1195. 3: YNUC15883 from Lev. 1197. 4: YNUC15884 from Lev. 1324. 5: YNUC15885 from Lev. 1196. 6: YNUC15886 from Lev. 1321. 7: YNUC15887 from Lev. 1316. 8: YNUC15888 from Lev. 1127. 9: YNUC15889 from Lev. 1197. 10: YNUC15890 from Lev. 1197. 11: YNUC15891 from Lev. 1191. 12: YNUC15892 from Lev. 1130. 13: YNUC15893 from Lev. 1323. 14: YNUC15894 from Lev. 1183. 15–16: YNUC15895–15896 from Lev. 1321. 17: YNUC15897 from Lev. 1323. 18: YNUC15898 from Lev. 1127. 19: YNUC15899 from Lev. 1321. 20: YNUC15900 from Lev. 1195. 21–24: YNUC15901–15904 from Lev. 1193. 25: YNUC15905 from Lev. 1128. 26: YNUC15906 from Lev. 1321. 27: YNUC15907 from Lev. 1193. 28: YNUC15908 from Lev. 1195. 29: YNUC15909 from Lev. 1193. 30: YNUC15910 from Lev. 1127. 31: YNUC 15911 from Lev. 1320.



- pl. 1, fig. 12.
- Cratognathodus kochi* (Huckriede), Mosher, 1968, p. 919, pl. 113, figs. 3, ?4, non fig. 7; Jenkins and Jenkins, 1971, non fig. 5, no. 29; Sahni and Chhabra, 1974, p. 263, 265, pl. 3, figs. D, ? E, F, non fig. 1; Gedik, 1975, p. 111–112, pl. 5, fig. 23; Budurov, 1976, pl. 4, fig. 29; Sudar, 1977, pl. 5, fig. 4; Catalov and Budurov, 1978, pl. 1, fig. 8; Koike, 1981, pl. 1, fig. 21; Koike, 1982, p. 20, pl. 9, fig. 15, non fig. 16; Önder, 1984, p. 76, pl. 22, figs. ?7, ?8.
- non *Prioniodina? kochi germanica* Kozur, 1968a, p. 139–140, pl. 1, figs. 24, 25; Kozur, 1968b, pl. 3, figs. 15, 19, 21; Kozur, 1968c, p. 1081.
- Cratognathodus cuspidatus* Koike, 1982, p. 20–21, pl. 9, figs. ?17, 18.
- Pb element**
- Ozarkodina saginata* Huckriede, 1958, p. 153–154, pl. 13, figs. 16, 17, 20; Mosher, 1968, p. 932, pl. 115, fig. ?14, non fig. 15.
- Pseudoozarkodina saginata* (Huckriede), Vrielynck, 1987, p. 229–230, pl. 14, figs. 9–11.
- Cratognathodus posterognathus* Mosher, 1968, p. 919, pl. 113, figs. 10, 14; Koike, 1973, p. 98, pl. 17, figs. 30, 31; Budurov and Stefanov, 1975, pl. 1, fig. ?35; Koike, 1981, pl. 1, fig. 30; Koike, 1982, p. 20, pl. 9, figs. 20, 21; Önder, 1984, p. 77, pl. 22, figs. 9–11.
- Lonchodina? posterognathus* (Mosher), Kozur and Mostler, 1971, pl. 1, fig. 10; Mock, 1971, pl. 1, fig. 9; Kozur and Mostler, 1972, p. 19, pl. 10, figs. 6, 7, 11.
- Lonchodina angulata* Budurov, 1971, p. 28, pl. 1, figs. 5–9, 12; Čatalov and Budurov, 1975, p. 1248, pl. 1, fig. 8.
- Cratognathodus posterognathus posterognathus* Mosher, Gedik, 1975, p. 112, pl. 5, figs. 19, 20, 22.
- Cratognathodus posterognathus angulatus* (Budurov), Gedik, 1975, p. 113, pl. 8, figs. 25, 26.
- Cratognathodus angulatus* (Budurov), Budurov, 1976, pl. 4, figs. 17, 18; Čatalov and Budurov, 1978, pl. 1, fig. 2.
- M element**
- Lonchodina venusta* Huckriede, 1958, p. 152–153, pl. 11, fig. 25; Spasov and Ganey, 1960, p. 82, pl. 1, figs. 15–17; Hirsch, 1969, pl. 1, fig. 5.
- Cypridodella venusta* (Huckriede), Mosher, 1968, p. 922–923, pl. 114, figs. 1, 7, ?13; Gedik, 1975, p. 115–116, pl. 7, figs. 16–18; Koike, 1982, p. 23, pl. 7, fig. 47; Önder, 1984, p. 78–79, pl. 22, figs. 5, 6.
- Prioniodina* (*Cypridodella*) *venusta* (Huckriede), Kozur and Mostler, 1971, pl. 1, figs. 3, 4; Mock, 1971, pl. 2, figs. 5, 10, 11; Kozur and Mostler, 1972, p. 32, pl. 11, figs. 16, 24, pl. 12, fig. 11, pl. 15, fig. 3.
- Prioniodina venusta* (Huckriede), Čatalov and Budurov, 1975, p. 1248, pl. 1, fig. 12; Budurov, 1976, pl. 4, figs. 23–26; Sudar, 1977, pl. 5, fig. 9; Čatalov and Budurov, 1978, pl. 1, fig. 1; Vrielynck, 1987, p. 226–228, pl. 10, fig. 15, pl. 11, figs. 1, 2.
- ? *Cypridodella pronoides* (Budurov), Koike, 1982, p. 22, pl. 7, figs. 48, 49.
- Sa element**
- Roundya lautissima* Huckriede, 1958, p. 160, pl. 11, fig. 41, pl. 13, figs. 13, 15; Spasov and Ganey, 1960, p. 90, pl. 2, figs. 15, 22.
- Diplododella lautissima* (Huckriede), Ishii and Nogami, 1966, pl. 1, fig. 15; Mosher, 1968, p. 924, pl. 114, fig. 20; Koike, 1973, p. 101, pl. 17, fig. 32; Sahni and Chhabra, 1974, p. 270, pl. 3, fig. ?S; Budurov, 1976, pl. 4, fig. 36; Sudar, 1977, pl. 5, fig. 2.
- Hibbardella lautissima* (Huckriede), Mosher and Clark, 1965, p. 561, pl. 65, figs. ?1, ?3, ?4; Kozur and Mostler, 1971, pl. 1, fig. 13; Mock, 1971, pl. 3, figs. 7, 13; Kozur and Mostler, 1972, p. 12, pl. 9, fig. 10, pl. 12, figs. 10, 13; Vrielynck, 1987, p. 195–196, pl. 11, figs. 3–7.
- pars *Hibbardella magnidentata* (Tatge), Gedik, 1975, p. 122–123, pl. 4, figs. 8–10 (only).
- Sb₁ element**
- Apatognathus* sp. Huckriede, 1958, p. 147, pl. 11, fig. 29.
- ? *Hindeodella stoppeli* Bender, 1967, p. 510, pl. 2, figs. 6, 15–17.
- pars *Prioniodina petrae-viridis* (Huckriede), Mosher, 1968, p. 934–935, pl. 116, figs. 30, 31 (only).
- pars *Enantiognathus petraeviridis* (Huckriede), Kozur and Mostler, 1972, p. 9, pl. 10, figs. 1, 2, pl. 14, figs. 4, 5, 8, 12 (only).
- Sb₂ element**
- Lonchodina spengleri* Huckriede, 1958, p. 152, pl. 10, figs. 54, ? 55, ?56, pl. 11, fig. 6, pl. 12, fig. 9, pl. 13, figs. 1, 6, 10, pl. 14, fig. 11; Budurov, 1962, p. 119, pl. 1, figs. ?5–8; Mosher and Clark, 1965, p. 562, pl. 66, fig. ?5; Bender, 1967, p. 513–514, pl. 3, figs. 12, ?13–15, non fig. 17.
- Prioniodina spengleri* (Huckriede), Čatalov and Budurov, 1975, p. 1248, pl. 1, fig. ?13, non fig. 14; Sudar, 1977, pl. 5, fig. ?11; Čatalov and Budurov, 1978, pl. 1, fig. 5, non figs. 4, 6, pl. 2, fig. 20, non figs. 19, 21.
- Prioniodina spengleri* (Huckriede), "dimitrovi" element, Budurov, 1976, pl. 3, figs. 8, 18.
- Prioniodina spengleri* (Huckriede), "spengleri" element, Budurov, 1976, pl. 3, figs. ?9, ?11–15, 16–18, non figs. 20–25, non pl. 4, figs. 37–39.
- Prioniodina* (*Flabellignathus*) *spengleri sapanlii* Gedik, 1975, p. 146–147, pl. 7, figs. 22, 26, 27, 30.
- Cypridodella spengleri* (Huckriede), Mosher, 1968, p. 922, pl. 113, figs. 19, 20, 25, non fig. 18; Koike, 1973, p. 100, pl. 16, fig. 31; Sahni and Chhabra, 1974, p. 269, fig. 3–?O; Önder, 1984, p. 78, non pl. 22, figs. 3, 4.
- Hindeodella* (*Metaproniodus*) *spengleri* (Huckriede), Kozur and Mostler, 1971, pl. 1, fig. 12; Mock, 1971, pl. 2, fig. ?13, non fig. 14; Kozur and Mostler, 1972, p. 16–17, non pl. 7, fig. 11, pl. 10, fig. 4, pl. 15, figs. 1, 5.

→ **Figure 4.** Pb, M, Sa, and Sb₁ elements of *Cratognathodus multiamatus* (Huckriede) from the Tahoe Formation, all × 60. **1–14**, Pb elements, 1: YNUC15912 from Lev. 1191. 2: YNUC15913 from Lev. 1321. 3–5: YNUC15914–15916 from Lev. 1130. 6: YNUC15917 from Lev. 1321. 7: YNUC15918 from Lev. 1316. 8: YNUC15919 from Lev. 1321. 9: YNUC15920 from Lev. 1322. 10: YNUC15921 from Lev. 1193. 11: YNUC from Lev. 1130. 12: YNUC 15923 from Lev. 1316. 13: YNUC15924 from Lev. 1197. 14: YNUC15925 from Lev. 1192. **15–19**, M elements, 15: YNUC15926 from Lev. 1321. 16: YNUC15927 from Lev. 1197. 17: YNUC15928 from Lev. 1323. 18: YNUC15929 from Lev. 1193. 19: YNUC15930 from Lev. 014. **20–24**, Sa elements, 20: YNUC15931 from Lev. 016. 21: YNUC15932 from Lev. 1127. 22: YNUC15933 from Lev. 1129. 23: YNUC15934 from Lev. 1193. 24: YNUC15935 from Lev. 1195. **25–32**, Sb₁ elements, 25: YNUC15936 from Lev. 1197. 26–27: YNUC15937–15938 from Lev. 1196. 28–29: YNUC15939–15940 from Lev. 1197. 30: YNUC15941 from Lev. 1196. 31–32: YNUC15942–15943 from Lev. 1197.



Sc₁ element

Hindeodella petrae-viridis (Huckriede, 1958, p. 149-150, pl. 11, fig. ? 46, pl. 13, figs. ?7, ?8, 9, 11, 12, 14, pl. 14, fig. 6, non fig. 7; Spasov and Ganey, 1960, p. 81, pl. 1, figs. 3, 4; Budurov, 1962, p. 116, pl. 1, figs. ?19, ?20; Mosher and Clark, 1965, p. 562, pl. 65, fig. ?9; Ishii and Nogami, 1966, pl. 1, fig. ?14; Catalov and Stefanov, 1966, pl. 1, figs. 4, 7, ?16; Hirsch, 1969, pl. 1, fig. 4.

Prioniodina petrae-viridis (Huckriede), Mosher, 1968, p. 934-935, pl. 116, figs. 28, 29, non figs. 30, 31; Sahni and Chhabra, 1974, p. 284-285, fig. 5, ?A, C, ?D, ?E; Sudar, 1977, pl. 5, figs. ?7, ?12; Önder, 1984, p. 86-87, pl. 23, figs. 16-21.

Prioniodina (Flabellignathus) petraeviridis (Huckriede), Gedik, 1975, p. 145-146, pl. 8, figs. 11, 27.

Prioniodina spengleri (Huckriede), "petraeviridis" element, Budurov, 1976, pl. 4, figs. 38, 39, non fig. 37.

Parachirognathus petrae-viridis (Huckriede), Bender, 1967, p. 524, pl. 5, figs. ?1, 2, 3, ?4, ?5, 6, non figs. 8, 9.

Enantiognathus petraeviridis (Huckriede), Mock, 1971, pl. 1, fig. 3, non figs. 4, 10, pl. 2, fig. 17; Kozur and Mostler, 1972, p. 9, pl. 10, fig. ?3, non figs. 1, 2, pl. 12, fig. ?16, non pl. 14, figs. 4, 5, 8, 12; Kemper et al., 1976, pl. 6, fig. ?8; Vrielynck, 1987, p. 188, pl. 9, fig. ?10, non figs. 11, 12.

Diplododella petraeviridis (Huckriede), Koike, 1981, pl. 1, fig. 26; Koike, 1982, p. 26-27, pl. 7, fig. 25.

Prioniodina (Flabellignathus) latidentata (Tatge), Gedik, 1975, p. 143-144, pl. 8, figs. 13-15, ?16-18, ?20, ?21, ?23, ?24.

pars *Hindeodella (Metaproniodus) spengleri* (Huckriede), Kozur and Mostler, 1972, p. 16-17, pl. 1, fig. 11 (only).

Sc₂ element

Hindeodella multihamata (Huckriede, 1958, p. 148-149, pl. 10, figs. 52, 53, pl. 12, fig. 23; Catalov and Stefanov, 1966, pl. ?1, fig. 15; Bender, 1967, p. 508-509, pl. 2, figs. ?18, 20; Mosher, 1968, p. 925, pl. 114, fig. 19; Kozur and Mostler, 1971, pl. 1, fig. 9; Koike, 1973, p. 104, pl. 17, figs. 26-29, non fig. 25; Sahni and Chhabra, 1974, p. 274-275, fig. 4, A, D; Budurov, 1976, pl. 4, fig. 40; Chhabra, 1981, pl. 1, figs. 14, 17; Koike, 1982, p. 30, pl. 9, figs. 23, 25, non fig. 24; Vrielynck, 1987, p. 201-202, pl. 14, fig. ?6, non figs. 4, 5.

Neohindeodella multihamata (Huckriede), Koike, 1981, pl. 1, fig. 17. *Hindeodella (Metaproniodus) pectiniformis* (Huckriede), Kozur and Mostler, 1972, p. 15-16, pl. 5, figs. 1, 2, pl. 14, figs. 19, ?23, 24.

Prioniodina (Flabellignathus) pectiniformis (Huckriede), Gedik, 1975, p. 144-145, pl. 8, fig. 22.

Prioniodina libita Mosher, 1968, p. 934, pl. 115, figs. 17, 26, 29; Önder, 1984, p. 86, pl. 23, figs. 13, 14.

Description.—Pa and Pb elements have common morphologic characteristics such as stout unit, broad cusp, and discrete denticles. M, Sa, Sb₁, Sb₂, Sc₁, and Sc₂ elements possess long cusp, and thin process with long denticles. All elements possess distinct basal cavity.

Pa element: Paired segminate elements with arched and

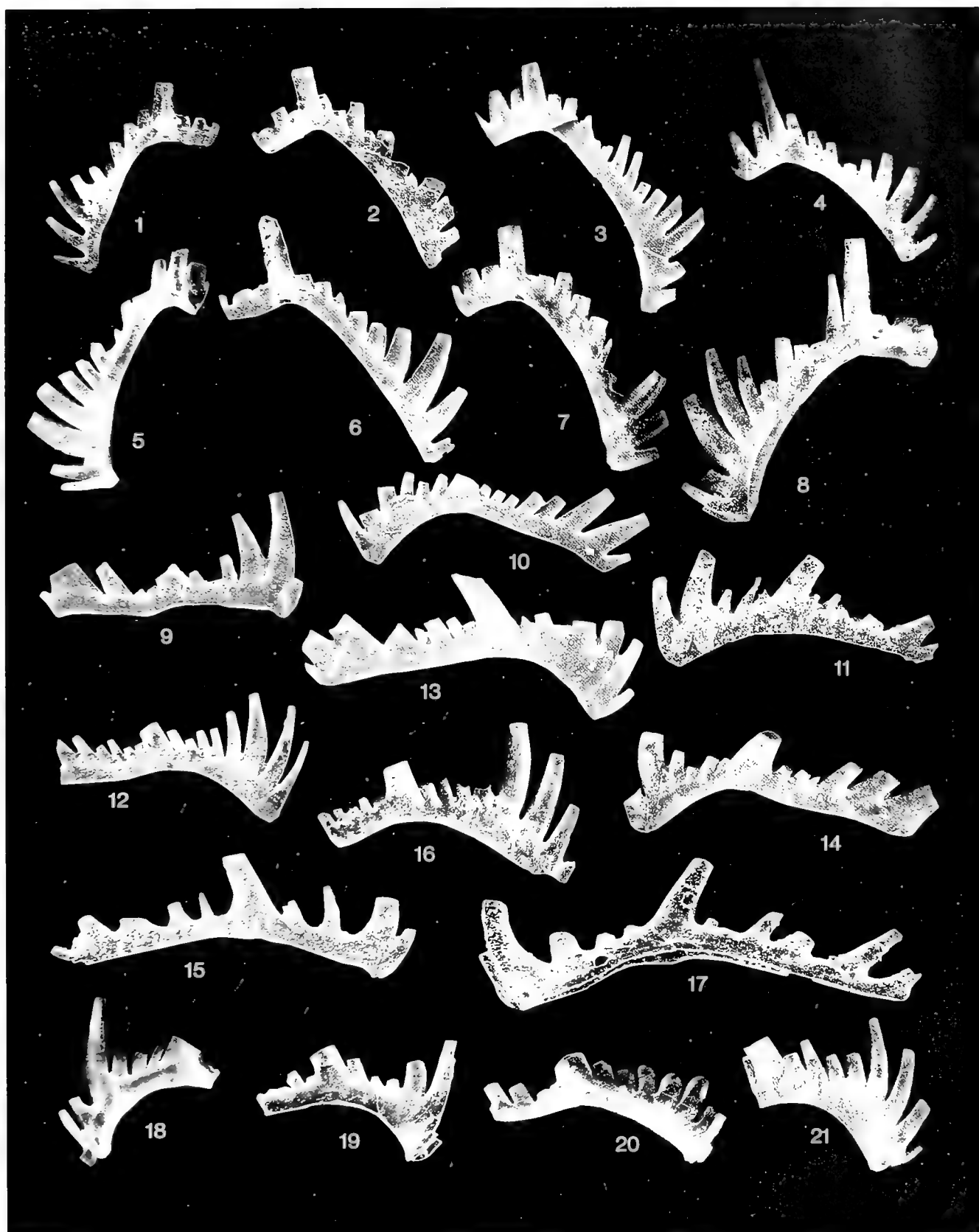
laterally curved process. Length of anterior process ranges from 250 to 720 μm . Anterior process relatively low to high and carries 3 to 10 denticles. Denticles represent broad variation in denticulation and size: narrowly to broadly discrete and subequal to highly unequal in size. In the case of consisting of highly unequal denticles, they tend to become larger in central portion on anterior process in some specimens and become larger toward anterior in others. One or two denticles may be present behind cusp. Cusp shows a morphologic variation in relative size, shape, and degree of inclination: narrow to broad, short to long, and medium-angled to subparallel with anterior process. Basal cavity shallow, narrowly to widely expanded laterally. Basal cavity margin thin in immature form and tends to be thick in mature form. Basal groove narrow and extends from basal cavity to anterior end.

Pb element: paired angulate element with subequal anterior and posterior processes in length. Both processes meet at an angle of about 120 to 160 degrees in both upper and lateral views. Posterior process may be convex inward. Length of anterior and posterior processes ranges from 160 to 400 μm , respectively. Denticles on anterior process 3 to 6 in number, short, discrete, and tend to increase in length and inclination posteriorly. Denticles on posterior process 3 to 6 in number, short, slender, discrete, and tend to increase in length and inclination posteriorly. Cusp large and stands commonly on anterior process and uncommonly on posterior process. Basal cavity a laterally compressed lenticular shape flaring outward in lower view. Basal groove extends anteriorly and posteriorly from basal cavity to beneath processes.

M element: Paired breviform digyrate elements with short and long lateral processes ranging from 60 to 140 μm and from 530 to more than 670 μm in length, respectively. Both processes meet at an angle of about 80 to 100 degrees in antero-posterior views. Short lateral process may be convex inward and carries 1 to 3 short denticles or none in some specimens. Long lateral process projects strongly downward and slightly convex outward. Denticles on long lateral process 8 to 10 in number, curve inward, and tend to increase in size and inclination downward. Cusp large and curves posteriorly. Basal cavity expanded posteriorly and slightly depressed on anterior side. Small lip of basal cavity present on posterior side and rounded keel extends from basal margin of lip to halfway up cusp. Narrow basal groove beneath both processes extends into basal cavity.

Sa element: Alate elements with two long lateral processes and long posterior process. Length of each lateral process ranges from 160 to 250 μm . Length of posterior process unknown due to its incompleteness and more than 330 μm in moderately large specimens. Lateral processes form an angle of 60 to 90 degrees with each other in anterior

→ **Figure 5.** Sb₂, Sc₁ and Sc₂ elements of *Cratognathodus multihamatus* (Huckriede) from the Tahoe Formation. all $\times 60$. 1-8, Sb₂ elements, 1-2: YNUC15944-15945 from Lev. 1316. 3: YNUC15946 from Lev. 1321. 4: YNUC15947 from Lev. 1323. 5: YNUC15948 from Lev. 1321. 6: YNUC15949 from Lev. 1191. 7: YNUC15950 from Lev. 1321. 8: YNUC15951 from Lev. 1183. 9-17, Sc₂ elements, 9-15: YNUC15952-15958 from Lev. 1197. 16: YNUC15959 from Lev. 1193. 17: YNUC15960 from Lev. 1197. 18-21, Sc₁ elements, 18: YNUC15961 from Lev. 1127. 19: YNUC15962 from Lev. 1191. 20: YNUC15963 from Lev. 1322. 21: YNUC15964 from Lev. 1127.



view and 90 to 120 degrees with posterior process in lateral view. Denticles on each lateral process 3 to 5 in number, discrete, tend to be large in central portion. Inclination of denticles tends to increase toward cusp. Denticles on posterior process more than 11 in number, short, indiscrete and standing perpendicular. Cusp as long as largest denticle on lateral processes and slightly curves posteriorly. Basal cavity moderately expanded and narrow basal groove extends beneath lateral and posterior processes.

Sb₁ element: Paired breviform digyrate elements with subequal, long, slender lateral processes. Length of each lateral process ranges from 170 to 450 μ m. Both processes meet at an angle of about 90 to 120 degrees in upper view and are convex anteriorly. Denticles on each lateral process 7 to 10 in number, indiscrete, slightly inclined posteriorly, and tend to increase in length distally, the largest being the distalmost 2nd or 3rd. Cusp slender and as large as largest denticle on lateral processes. Basal cavity slitlike, narrow basal groove extends from basal cavity toward lateral processes.

Sb₂ element: Paired extensiform digyrate elements with short and long lateral processes. Length of short and long processes ranges from 130 to 200 μ m and from 460 to 640 μ m, respectively. Both processes meet at an angle of 100 to 130 degrees in antero-posterior views. Denticles on short lateral process 2 to 5 in number and tend to increase in length and inclination toward cusp. Denticles on long lateral process 10 to 13 in number, weakly curve posteriorly, and tend to increase in length distally, the largest being the distalmost 3rd or 4th. Inclination of denticles tends to increase toward cusp. Cusp slender, as large as large denticles on long lateral process, and slightly curves posteriorly. Basal cavity forms triangular shape in lower view. Small lip of basal cavity present on posterior side and narrow keel extends from basal margin of lip to approximately halfway up cusp. Narrow basal groove extends from basal cavity to beneath both lateral processes.

Sc₁ element: Paired bipennate elements with bifurcate long anterior process and long posterior processes. Length of anterior process ranges from 230 to 370 μ m. Length of posterior process cannot be measured because of its incompleteness. Anterior process bends at an angle of 30 to 80 degrees downward and 10 to 20 degrees inward. Denticles on anterior process 5 to 8 in number, tend to increase abruptly in size, being largest in anterior to middle portion, and then decreasing in size posteriorly. Bifurcation projects anterolaterally and forms an angle of about 160 degrees in both upper and lateral views and carries 1 to 3 small, discrete denticles. Posterior process may carry almost the same number of denticles as on anterior process. Cusp as long as longest denticle on anterior process. Basal cavity slitlike, narrow basal groove extends toward anterior and posterior processes.

Sc₂ element: Paired bipennate elements with long, slender anterior and posterior processes with long, discrete denticles. Length of anterior and posterior processes ranges from 300 to 470 μ m and 380 to 750 μ m, respectively. Anterior process bends at an angle of 30 to 80 degrees downward and 10 to 30 degrees inward. Denticles on

anterior process 5 to 9 in number and tend to be largest in anterior to middle portion and increase in inclination posteriorly. Denticles on posterior process 5 to 12 in number and tend to increase in size and inclination posteriorly. Basal cavity slitlike, very small lip of basal cavity turned upward on inner side. Narrow groove extends from basal cavity toward anterior and posterior processes.

Remarks.—The "ozarkodiniiform" element of *Celsigondolella watznaueri watznaueri* (Kozur) is somewhat similar to the Pa element of *Cr. multihamatus*. The former has, however, a conspicuously long cusp whose feature is out of the range of morphologic variation of the latter. The form species *Pollognathus sequence* (Kozur) and *P. germanicus* (Kozur) fairly resemble the Pa element of *Cr. multihamatus* but the former have a relatively long and slender cusp.

The holotype and other specimens of the form species *Ozarkodina saginata* illustrated by Huckriede (1958) are all incomplete and lack most of their posterior processes, which has caused some confusion in determination among angulate elements. The stout unit with relatively long discrete denticles of *O. saginata* shares characteristics with the Pb element of *Cr. multihamatus*. The holotype and another specimen of the form species *Cratognathodus posterognathus* (=the Pb element of *Cr. multihamatus*) shown by Mosher (1968) are of young forms of the form species *Or. saginata*.

One specimen figured as the form species *Lonchodina venusta* (=the M element of *Cr. multihamatus*) by Huckriede (1958) is incomplete and lacks the distal half of the longer lateral process but well represents such characteristic morphology as long denticles on the lateral process and broadly expanded basal cavity.

All specimens previously figured as the form species *Diplododela lautissima* and specimens determined by me as the Sa element of *Cr. multihamatus* lack most of their posterior processes. The Sa element can be distinguished, however, from the form species *D. magnidentata* (Tatge) by the anteriorly projecting lateral processes with long discrete denticles.

The specimens illustrated as the form species *Hindeodella stoppeli* by Bender (1967) are all incomplete but they appear to correspond to the Sb₁ element of *Cr. multihamatus* because of their "enantiognathiform" digyrate type with a broad angled junction of the lateral processes.

All specimens including the holotype of the form species *Lonchodina spengleri* (the Sb₂ element of *Cr. multihamatus*) are incomplete and lack most of the longer lateral process. The identification of this element is, however, not so difficult because of its extensiform digyrate type and the presence of a triangular basal cavity.

The holotype of the form species *Hindeodella petraeviridis* (=the Sc₁ element of *Cr. multihamatus*) illustrated by Huckriede (1958) is of a part of the anterior process and lacks the bifurcation on the anterior processes. Therefore, some workers regarded this form species as bipennate type without the bifurcate anterior process or breviform digyrate types. The holotype possesses, however, a faint trace of the bifurcation on the basal part of the anteriormost denticle. Huckriede (1958) claimed that the form species *H. petraeviridis* is characterized by the presence of the bifurcation on

the anterior process and four specimens figured by Huckriede (1958) carry distinct bifurcation. It is very difficult to distinguish Sc_2 from Sc_1 elements of *Cr. multihamatus* if the Sc_2 elements are incomplete and lack the anterior portion of their anterior processes.

The form species *Prioniodella pectiniformis* erected by Huckriede (1958) is based on the specimens of a part of the posterior process with long discrete denticles. The features agree well with those of Sc_2 elements of *Cr. multihamatus*.

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Evolutionary history of the Cenozoic bivalve genus *Kaneharaia* (Veneridae)

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Abstract. The evolutionary history of the bivalve genus *Kaneharaia* (Dosiniinae) is discussed. The genus *Kaneharaia* is restricted to the North Pacific region and contains four species: *K. kaneharai* (Yokoyama), *K. kannoi* (Masuda), *K. ausiensis* (Ilyina) and *K. sp.* *K. ausiensis* survived until the mid Pliocene while the other three species became extinct at the end of the Miocene. In addition to these species, *Dosinia mathewsonii* from the upper Oligocene San Ramon Formation of California and *D. whytneyi* from the early middle Miocene Astoria Formation of Oregon most probably belong to the genus *Kaneharaia*. *Kaneharaia* evolved from the common ancestor with *Dosinia* because both genera share many common characteristics such as the subumbonal pit, the brown-coloured surface, and the finely crossed lamellar structure in the outer layer. Based on the fossil record, *Kaneharaia* first appeared in the northeastern Pacific during the late Oligocene and migrated westward during the early middle Miocene Climatic Optimum in the North Pacific.

Key words: Bivalvia, evolution, *Kaneharaia*, *Dosinia*, Dosiniinae

Introduction

Kaneharaia is an extinct genus of Dosiniinae (Bivalvia: Veneridae) which was first proposed as a subgenus of *Dosinia* Scopoli, 1777 by Makiyama (1936), based on *Dosinia kaneharai* Yokoyama, 1926 from the Miocene Kanomatazawa Formation in Tochigi Prefecture as its type species. Species of *Kaneharaia* have been found in the Miocene deposits of Honshu and Hokkaido, Japan, Sakhalin and Kamchatka, Russia and northern Korea, and also in the lower Pliocene of Honshu (Masuda, 1967; Amano, 1983; Gladenkov *et al.*, 1987; Amano and Sato, 1995). Other than *K. kaneharai*, the following species and subspecies of *Kaneharaia* have been described: *K. kaneharai* (Yokoyama, 1926), *K. ausiensis* (Ilyina, 1954), *K. kaneharai ouchiensis* (Kanno, 1955), *K. kannoi* (Masuda, 1963), *K. kaneharai fujinensis* (Masuda, 1967), *K. kaneharai rumoiensis* (Amano, 1983), *K. kaneharai uandiensis* (Sinelnikova, 1987 in Gladenkov *et al.*, 1987).

Makiyama (1936) and Masuda (1967) pointed out that *Kaneharaia* is similar to *Dosinidia* Dall, 1902 (= *Dosinia* Scopoli, 1777) in the absence of escutcheon and lamellated concentric sculpture which are common characters in other Japanese dosiniine genera such as *Phacosoma* Jukes Brown, 1912, *Dosinella* Dall, 1902 and *Dosinorbis* Dall, 1902. However, no detailed comparison of hinge structure between *Kaneharaia* and *Dosinia* has been made.

When they examined the shell microstructure of *Kanehar-*

aia kaneharai and *Phacosoma* spp., Kobayashi *et al.* (1968) and Hikida (1996) showed that the shell microstructure is a useful character for diagnosing some genera within Dosiniinae and separated *Kaneharaia* from *Phacosoma* as a distinct genus based on the difference of microstructure of the outer layer: spherulitic structure in *Kaneharaia* and composite prismatic structure in *Phacosoma*. However, these authors did not examine the shell microstructure of dosiniine species from the Cenozoic of the North Pacific, including *K. ausiensis*.

Thus, the lack of enough information on hinge structure and shell microstructure prevents us from understanding the detailed relationship among the *Kaneharaia* and other dosiniines from the Cenozoic of the North Pacific.

Recently, it has become clear that some molluscan genera originated in the northeastern Pacific and then migrated to the northwestern Pacific during the early middle Miocene (Vermeij, 1991; Amano *et al.*, 1993; Matsubara, 1994; Reid, 1996; Amano and Vermeij, 1998; Amano, 1998). If we can make clear the close phylogenetic relationship between *Kaneharaia* and the American *Dosinia* species, it should be possible to judge whether *Kaneharaia* is another example of a westward spreading genus or not.

Fortunately, we were able to collect some well preserved specimens of *Kaneharaia ausiensis* (Ilyina) from the Miocene of Sakhalin and also examined previously undocumented specimens of *K. ausiensis* from the Pliocene of Hokkaido and of *K. sp.* from the Miocene of Kodiak Island. Here we

examine the morphology of this material in detail and the shell microstructure of *K. ausiensis* and the Recent *Dosinia* species as well in order to clarify the evolutionary history of *Kaneharaia*.

Materials

A number of fossil specimens identified as *Kaneharaia ausiensis* were collected from the following four localities (Figure 1): Loc. 1, river bank about 2 km upstream of Lesnaya River in southeastern Sakhalin; early middle Miocene Ausinskaya Formation: Loc. 2, roadside cliff about 2.5 km north of Baykovo in southwestern Sakhalin (the type locality of *Dosinia ausiensis* Ilyina, 1954); early middle Miocene Ausinskaya Formation: Loc. 3, roadside cliff about 500 m northwest of Kotobuki Bridge in Kamitokushibetsu, Hokkaido; middle Miocene Shibiutan Formation: Loc. 4, bank of the Horonitachibetsu River near Numata dai-go in Hokkaido; early Pliocene Horokaoshirika Formation yielding the Pliocene index fossil, *Fortipecten takahashii* (Yokoyama). These specimens are housed at Joetsu University of Education (JUE).

Five fossil specimens identified as *Kaneharaia* sp. were

provided by Emeritus Professor Saburo Kanno of the University of Tsukuba. These specimens are from the middle Miocene Ejoviy Horizon of Korf Bay in eastern Kamchatka and from the early middle Miocene Narrow Cape Formation on Kodiak Island, Alaska. Detailed information on these localities are unfortunately unknown. These are also stored in Joetsu University of Education (JUE). Besides these specimens, we examined the type specimens of *Kaneharaia kannoi* and *K. kaneharai fujinensis* stored in the Museum of Natural History of Tohoku University (IGPS).

We examined the shell microstructure of two fossil and four Recent species (Table 1).

Systematic notes on northern Pacific species

Family Veneridae Rafinesque, 1815
Subfamily Dosiniinae Deshayes, 1853
Genus *Kaneharaia* Makiyama, 1936

Comparison.—As pointed out by Makiyama (1936), Hatai (1938) and Masuda (1967), *Kaneharaia* and *Dosinia* share many features such as absence of the escutcheon and lamellated concentric ribs, and presence of a wide triangular

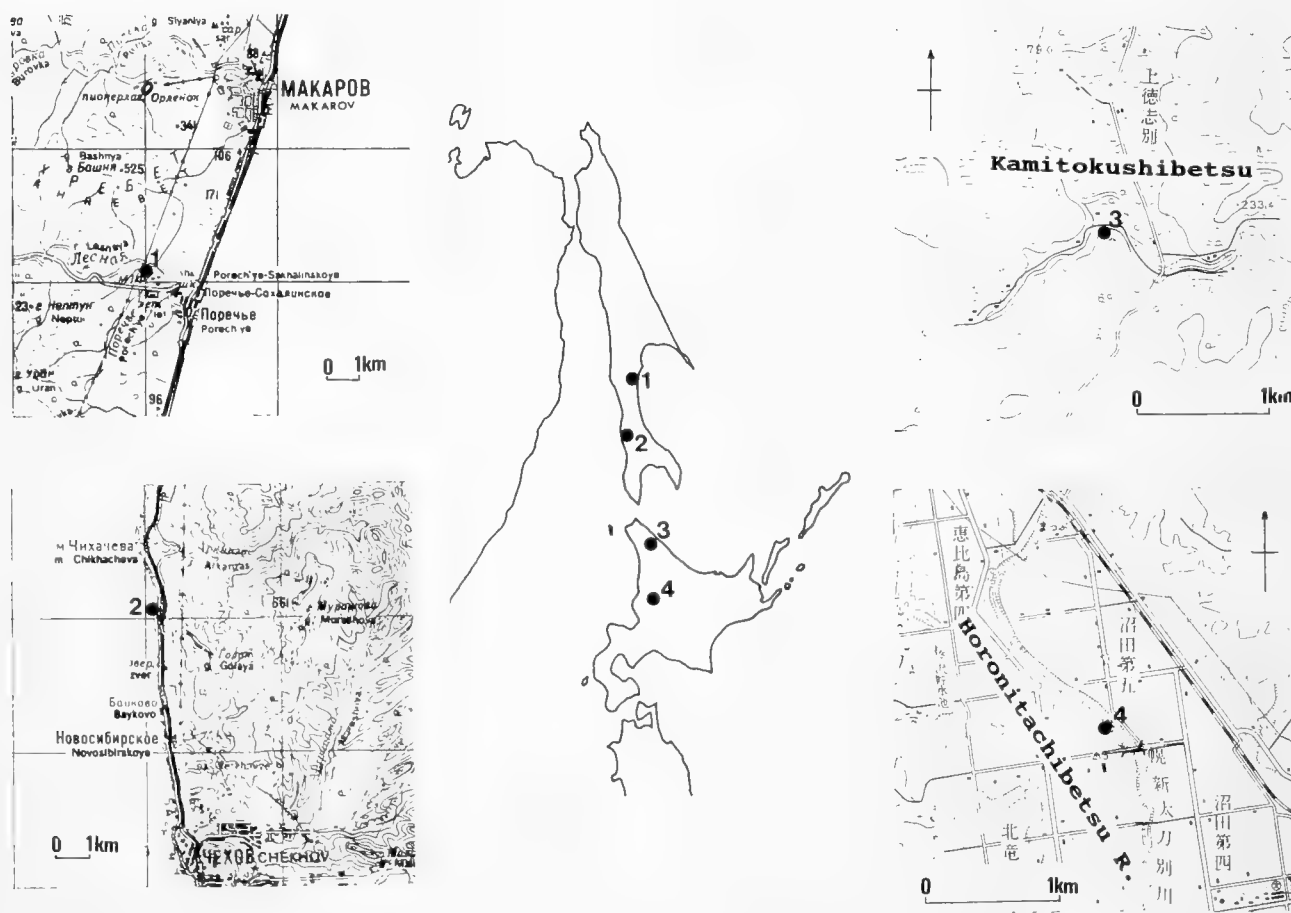


Figure 1. Collecting localities of *Kaneharaia* (using the topographical maps "Occhube" and "Moseushi", scale 1: 50,000, published by Geographical Survey of Japan).

Table 1. Shell structure of outer layer of Dosiniinae

| Species | SSO** | Age | Localities and formations |
|---|-----------|-------------|----------------------------------|
| * <i>Kaneharaia ausiensis</i> (Ilyina) | sph + fcl | Miocene | Ausinskaya F., Sakhalin (Loc. 1) |
| <i>K. kaneharai</i> (Yokoyama) | sph + fcl | Miocene | Kubota F., Fukushima Pref. |
| * <i>Dosinia discus</i> (Reeve) | fcl | Recent | Florida in USA |
| * <i>D. dunkeri</i> (Philippi) | fcl | Recent | Panama |
| * <i>D. ponderosa</i> (Gray) | fcl | Recent | California in USA |
| <i>Phacosoma japonicum</i> (Reeve) | cpr | Recent | Ohita Pref. |
| <i>P. japonicum</i> (Reeve) | cpr | Pleistocene | Omma F., Ishikawa Pref. |
| <i>P. japonicum</i> (Reeve) | cpr | Pliocene | Tatsunokuchi F., Miyagi Pref. |
| <i>P. troscheli</i> (Lischke) | cpr | Recent | Fukuoka Pref. |
| <i>P. tomikawensis</i> (Takagi) | cpr | Pleistocene | Omma F., Ishikawa Pref. |
| <i>P. tatunokutiensis</i> (Nomura) | cpr | Pliocene | Tatsunokuchi F., Miyagi Pref. |
| <i>P. hataii</i> (Masuda) | cpr | Miocene | Kubota F., Fukushima Pref. |
| * <i>P. akaisiana</i> (Nomura) | cpr | Miocene | Yatsuo G., Toyama Pref. |
| <i>P. kawagensis</i> (Araki) | cpr | Miocene | Mizunami G., Gifu Pref. |
| <i>P. nomurai</i> (Otuka) | cpr | Miocene | Mizunami G., Gifu Pref. |
| <i>Austrodosinia anus</i> (Philippi) | cpr | Recent | New Zealand |
| * <i>Pectunculus exoleta</i> (Linnaeus) | cpr | Recent | Galicia in Spain |

* Species treated in this study. The data of other species are based on Hikida (1996).

** Shell structure of outer layer (sph; spherulitic structure, fcl; finely crossed lamellar structure, cpr; composite prismatic structure, see also Hikida, 1996)

pallial sinus. In addition to these characters, we found that both genera have a subumbonal pit on the hinge plate (Figures 2 1–5, 13b, 3 1, 3, 6b, 11a) and sometimes have a brown-coloured shell surface.

The above features are not observed in *Phacosoma* Jukes-Brown, 1912, *Dosinella* Dall, 1902, *Dosinorbis* Dall, 1902 and *Austrodosinia* Dall, 1902 (Figures 3–2, 4, 5, 10; see also Fischer-Piette and Delmas, 1967). *Pectunculus* Da Costa, 1778 lacks not only the escutcheon, but also the subumbonal pit (Figure 3–8).

Morphologically, *Kaneharaia* differs from *Dosinia* by having a narrower thin plate above the nymph, a thick middle cardinal tooth of both valves, and a long anterior cardinal tooth in the left valve extending to the basal line of hinge plate.

As already pointed out by Kobayashi *et al.* (1968), Shimamoto (1986) and Hikida (1996), the inner layer throughout the Dosiniinae has the same microstructure (homogeneous structure). According to Hikida (1996), the outer layer of *Kaneharaia* is spherulitic in structure while in *Phacosoma*, *Austrodosinia*, *Pectunculus* and *Dosinella* the outer layer has a composite prismatic structure (Table 1).

We have found that the outer layer of *K. ausiensis* from Sakhalin (Loc. 1) has a spherulitic structure like *K. kaneharai*, but also was a finely crossed lamellar structure near the beak and ventral margin. On the other hand, the outer layers of *Dosinia discus* and *D. ponderosa* are composed totally of the finely crossed lamellar structure (Figure 4). On *D. ponderosa*, our observation supports the results by Carter and Lutz (1990), not by Taylor *et al.* (1973). Adding *D. dunkeri* to these two species, it has become clear that all the species of *Dosinia* here examined have the same finely crossed lamellar structure (Table 1). Thus, the outer shell microstructure of *Kaneharaia* has the features partly in common with *Dosinia*, but not with other dosiniines.

From the above morphological and shell microstructure data, we conclude that *Kaneharaia* is close to *Dosinia* than any other genus within the Dosiniinae.

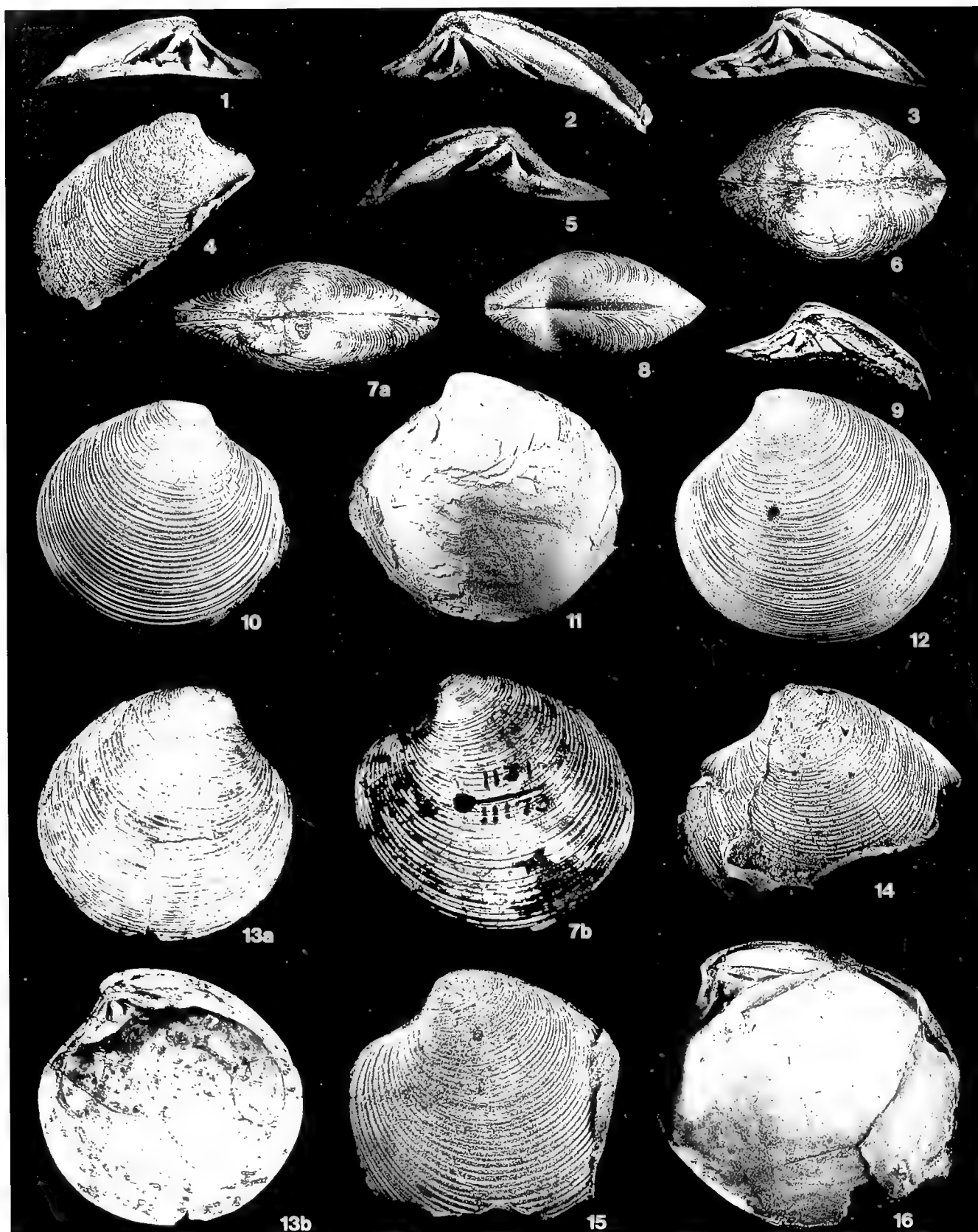
Remarks on American species.—*Dosinia mathewsonii* Gabb, 1869 was described from the upper Oligocene San Ramon Formation of California (Figure 2–7a, b). This species is characterized by the absence of the escutcheon, and presence of many wide concentric ribs, a subumbonal pit (Figure 2–9) on the hinge plate, and a brown-coloured shell surface. It is especially allied to *K. ausiensis* in having an almost identical shell shape and number of concentric ribs (15 between 10 mm and 20 mm from beak). Although no information on the pallial sinus shape of “*D.*” *mathewsonii* could be obtained, it is most probably included in the genus *Kaneharaia*.

When she examined the dosiniines from the early middle Miocene Astoria Formation in Oregon, Moore (1963) synonymized *Dosinia mathewsonii* with *Dosinia whitneyi* (Gabb, 1869). However, *D. whitneyi* is based on a single fragment. It is too difficult to obtain any information on the inner structure of *D. whitneyi*. For the above reasons, we do not use the species name *D. whitneyi*. The Astoria specimens would be better included in *Kaneharaia* rather than *Dosinia*, because the anterior cardinal tooth in the left valve extends to the basal line of the hinge plate and the plate above the nymph is narrow. However, there is also no information on pallial sinus shape in the Astoria specimens. Therefore, it is difficult to conclude whether the Astoria species can be accurately included in the genus *Kaneharaia*.

***Kaneharaia ausiensis* (Ilyina, 1954)**

Figures 2—1–5, 8, 10–12, 14–16; 3—14

Dosinia ausiensis Ilyina, 1954, p. 228, 229, pl. 18, figs. 7, 8; Zhidkova *et al.*, 1968, p. 107, 108, pl. 5, fig. 2, pl. 18, figs. 7, 8.



- Dosinia mirabilis* Uozumi (MS). Fujie *et al.*, 1964, pl. 6, fig. 4.
Dosinia (Kaneharaia) kaneharai kannoi Masuda. Masuda, 1967, pl. 2, fig. 9; Noda, 1992, p. 83, 84, pl. 4, fig. 1.
Dosinia (Kaneharaia) kaneharai rumoiensis Amano, 1983, p. 50, 51, pl. 4, fig. 12, pl. 5, figs. 1, 5, 10.
Dosinia (Kaneharaia) kaneharai uandiensis Sinelnikova in Gladenkov *et al.*, 1987, p. 35, pl. 7, figs. 4, 6.
Dosinia (Kaneharaia) ausiensis Ilyina. Gladenkov *et al.*, 1987, p. 35, fig. 3; Amano and Sato, 1995, p. 7, figs. 4-3, 6, 12; Amano *et al.*, 1996, p. 637, figs. 4-3, 8.
Dosinia (Kaneharaia) kaneharai Yokoyama. Shimizu and Fujii, 1995, fig. 6.

Type Locality.—Klyuch Bezimyanii (Japanese name, Ausi) in Chekhov district, southwestern Sakhalin (Loc. 2); early middle Miocene Ausinskaya Formation. Holotype, VNIGRI no. 7/6819.

Description of Sakhalin specimens.—Shell medium in size (47.4 mm in maximum length), suborbicular in outline, moderately inflated. Anterodorsal margin slightly concave, passing into well rounded ventral margin; posterodorsal margin broadly arcuate. Beak protruding, weakly prosogyrate, anteriorly situated. Surface sculptured by dense concentric ribs; concentric ribs 15–17 in number between 10 mm and 20 mm from beak, flattened near beak but becoming rounded and elevated near ventral margin. Lunule long, narrow, shallow, and not depressed by any distinct groove. Escutcheon lacking. Hinge plate consisting of one anterior lateral tooth and three cardinal teeth; middle cardinal tooth of right valve thick and simple; anterior lateral tooth of left valve rather large. Subumbonal pit small, situated at uppermost part of nymph plate. Pallial sinus rather shallow and triangular in shape.

Remarks.—The Sakhalin specimens have the same shell characters as the Hokkaido specimens other than shell size: the Pliocene Horokaoshirika specimen attains 60.6 mm in maximum length while that of the type specimen is 55 mm.

When they examined the fossil fauna from the Ausinskaya Formation in Novoselovo of southwestern Sakhalin, Amano *et al.* (1996) considered the following two subspecies to be junior synonyms of *D.(K.) ausiensis*: *D.(K.) kaneharai rumoiensis* Amano, 1983 and *D. (Kaneharaia) kaneharai uandiensis* Sinelnikova, 1987. They also considered that the specimens illustrated by Masuda (1967, pl. 2, fig. 9) and Noda (1992, pl. 4, fig. 1) as *D.(K.) kannoi* can be assigned to *D.(K.) ausiensis*.

Fujie *et al.* (1964) illustrated a specimen referred to *Dosinia mirabilis* Uozumi (MS) from the Miocene Tokushibetsu Formation in Hokkaido. Judging from its subcircular shell, fine concentric ribs and dentition with a subumbonal pit, this specimen should be referred to *K. ausiensis*.

Shimizu and Fujii (1995) illustrated a specimen of *D.(K.) kaneharai* Yokoyama from the "Otogawa fauna (type II)" of Toyama Prefecture. This specimen obviously has concentric ribs much more than the typical form of *K. kaneharai* and many elevated ribs near the ventral margin. Therefore, the Otogawa specimen should be referred to *K. ausiensis* rather than to *K. kaneharai*.

Comparison.—*Kaneharaia ausiensis* resembles *Kaneharaia kannoi* Masuda, 1963 from the lower middle Miocene Heiroke Formation of North Korea in having fine concentric ribs. However, *K. ausiensis* differs from *K. kannoi* (Figure 2–6) in its less inflated shell and more numerous concentric ribs (usually 12–13 between 10 mm and 20 mm from the beak in *K. kannoi*).

K. ausiensis differs from *K. kaneharai* Yokoyama in its orbicular rather than ovate shell and has much more numerous concentric ribs (15–17 between 10 mm and 20 mm from the beak instead of 8–12 in *K. kaneharai*).

Distribution.—Early middle Miocene Ausinskaya and Uandinskaya Formations in Sakhalin, and Chikubetsu Formation in Hokkaido; middle Miocene Togeshita, Tachikaraushinai and Shibiutan Formations in Hokkaido; late Miocene (?) "Otogawa Formation"; early Pliocene Horokaoshirika Formation in Hokkaido and Joshita Formation in Honshu.

Kaneharaia sp.

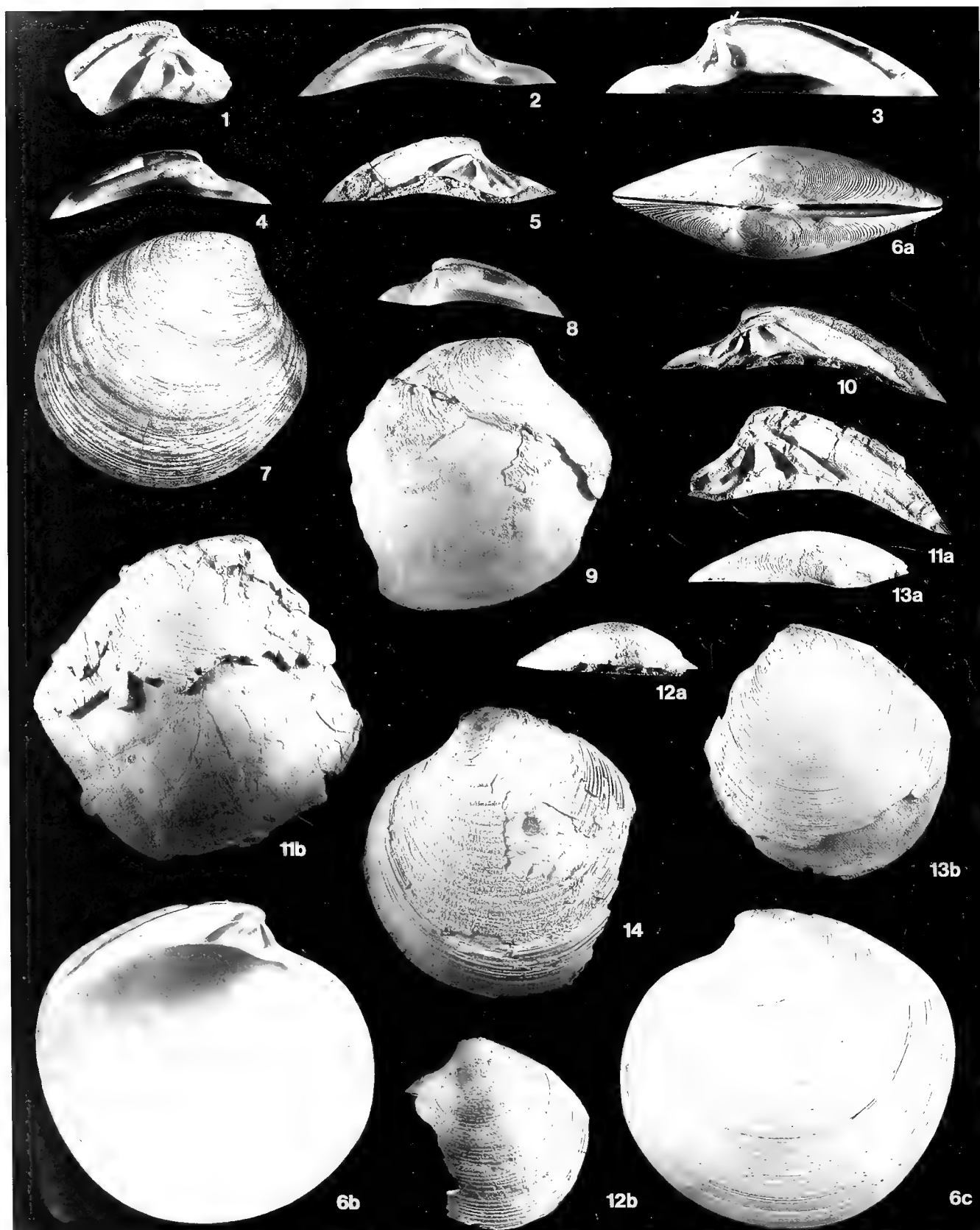
Figures 3–9, 11–13

- Dosinia* cfr. *mathewsoni* Gabb, Khomenko, 1933, p. 17, pl. 2, fig. 10, pl. 3, fig. 4.
Dosinia margaritana Wiedy, Slodkewitsch, 1938, pl. 88, figs. 3, 4.
 ? *Dosinia (Dosinia) whitneyi* Gabb, Moore, 1963, p. 73–74, pl. 24, figs. 3–10.
Dosinia (Kaneharaia) rumoensis Amano [sic], Gladenkov *et al.*, 1987, p. 34–35, pl. 8, figs. 1, 2, 4, 7–11.

Remarks.—Five specimens from eastern Kamchatka, Russia and Kodiak Island, Alaska resemble *K. ausiensis* in the absence of an escutcheon and lamellated concentric ribs and the presence of a wide pallial sinus and a narrow subumbonal pit. However, these specimens have more numerous (18–22) and more flattened concentric ribs than in *K. ausiensis*, and therefore they can easily be separated from the latter at the species level.

Khomenko (1933) recorded *Dosinia* cfr. *mathewsoni* Gabb, 1869 from Korf Bay of eastern Kamchatka, with which our specimens discussed here are identical. Thereafter, Slodkewitsch (1938) reassigned Komenko's specimens to *Dosinia margaritana* Wiedey, 1928. When they described the fauna from Korf Bay, Gladenkov *et al.* (1987) identified their speci-

← **Figure 2.** 1–5, 8, 10–12, 14 16: *Kaneharaia ausiensis* (Ilyina). 1; $\times 1.1$, JUE no. 15670–1: 3; $\times 1.2$, JUE no. 15670–2; Loc. 1, Ausinskaya F.; white arrow indicating a subumbonal pit. 2; $\times 1.05$, JUE no. 15666–3: 15; $\times 1.1$, JUE no. 15666–2; Loc. 3, Shibiutan F. 4; $\times 1.2$, JUE no. 15667–2: 5; $\times 1.15$, JUE no. 15667–3: 14; $\times 1$, JUE no. 15667–4: 16; $\times 1$, JUE no. 15667–5; Loc. 4, Horokaoshirika F. 8; $\times 1$, JUE no. 15664–5: 10; $\times 1$, JUE no. 15664–1: 12; $\times 1$, JUE no. 15664–3; Loc. 1, Ausinskaya F. 11; $\times 1$, JUE no. 15665–1, topotype, Loc. 2, Ausinskaya F. 6, 13: *Kaneharaia kannoi* (Masuda). 6; $\times 0.9$, IGPS no. 73203: 13a–b; $\times 0.8$, IGPS no. 64682, holotype, Heiroke F. 7a–b, 9: "*Dosinia*" *mathewsoni* Gabb. 7a–b; $\times 1$, UCMP no. 11173, San Ramon F.: 9; $\times 1$, UCMP no. 11149, reproduced from pl. 7, fig. 5 of Clark (1918), San Ramon F. White arrows in 1, 2, 3, 5, 9, 13b shows the subumbonal pit.



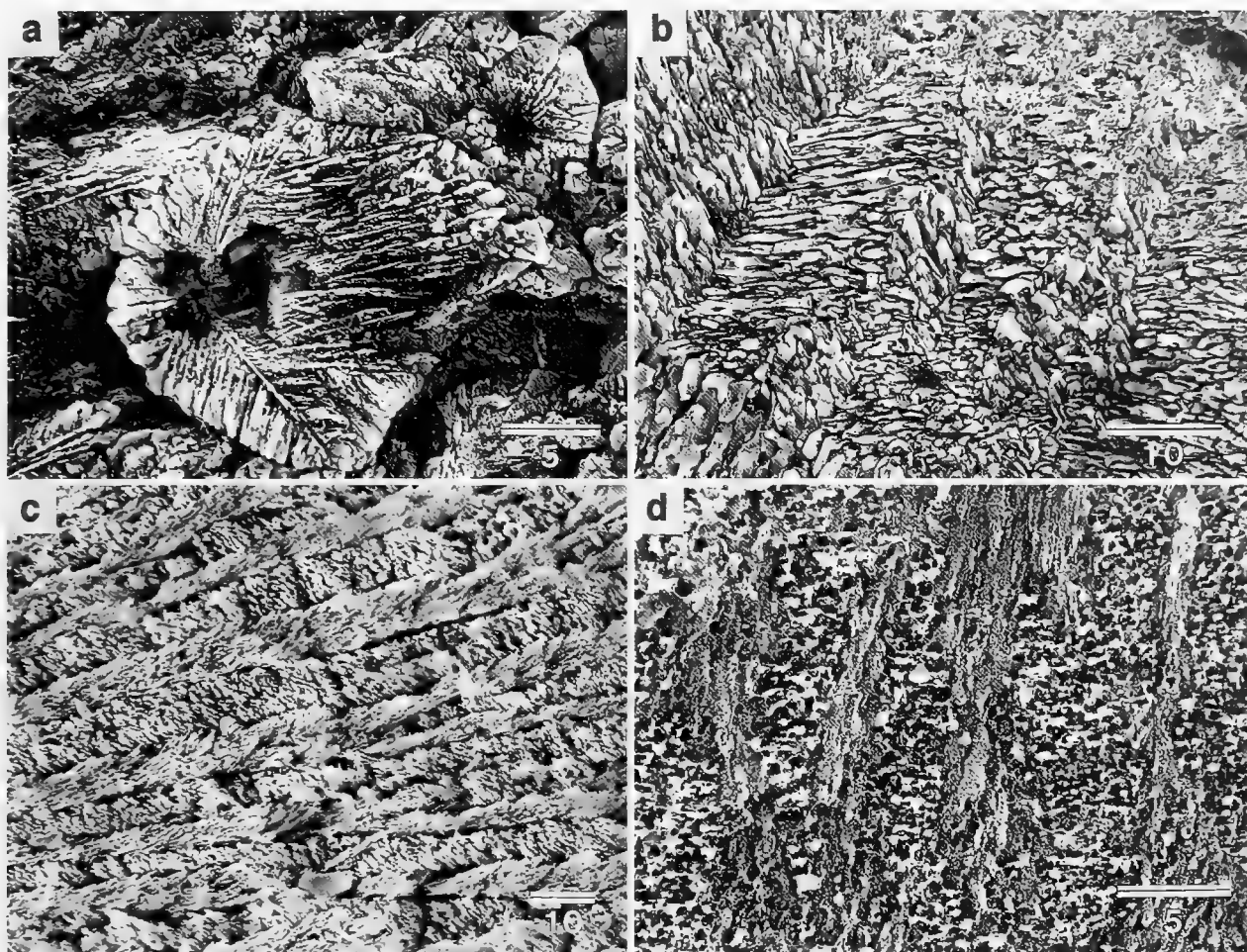


Figure 4. SEM photographs of shell microstructures of *Kaneharaia* and *Dosinia*; scale in μm ; polished and etched (with 0.6% (v/v) HCl; 10 sec.) section. **a**: Spherulitic structure of the outer layer of *Kaneharaia ausiensis* showing spherical to subspherical configuration of $3\text{--}12\ \mu\text{m}$ in diameter. The elongated structural subunits grow radially in all directions from central parts of the spherulite. The central parts appear to be etched more quickly than the surroundings. **b**: Finely crossed lamellar structure recognized near the beak of *K. ausiensis*. Acicular crystals aggregate to form a higher structural unit (first order lamella), and they are inclined in opposite directions in the adjacent first order lamellae. Long axes of the first order lamellae are arranged perpendicularly to the outer shell surface (upper right). **c**: Finely crossed lamellar structure of the outer layer of *Dosinia ponderosa*. The first order lamellae are arranged in a feathery, radial manner toward the ventral margin (shell surface). **d**: Finely crossed lamellar structure recognized near the beak of *Dosinia discus*. Individual first order lamellae are sometimes branched, their long axes being arranged perpendicularly to the outer shell surface.

← **Figure 3.** **1, 7**: *Kaneharaia kaneharai* (Yokoyama). **1**: $\times 1$, JUE no. 15671-2; **7**: $\times 0.8$, IGPS no. 90511; Loc. Tanagura, Kubota F. **2**: *Phacosoma japonicum* (Reeve), $\times 1$, JUE no. 15672, Loc. Tomikawa, Recent. **3**: *Dosinia ponderosa* (Gray), $\times 0.8$, UC Davis, Loc. Puerto Penasco, Sonora, Mexico, Recent. **4**: *Dosinella penicillata* (Reeve), $\times 1$, JUE no. 15673, Loc. Okayama, Recent. **5**: *Phacosoma tatunokutiensis* (Nomura), $\times 1$, JUE no. 15674, Loc. Tatsunokuchi, Tatsunokuchi F. **6a-c**: *Dosinia discus* (Reeve), $\times 1$, JUE no. 15675, Loc. Virginia Beach, USA, Norfolk F. **8**: *Pectunculus exoleta* (Linnaeus), $\times 1$, JUE no. 15676, Loc. Galicia, Spain, Recent. **9, 11-13**: *Kaneharaia* sp. **9**: $\times 1$, JUE no. 15668-2; **13a-b**, $\times 1$, JUE no. 15668-1; Loc. Kodiak Is., USA, Narrow Cape F. **11a**: $\times 1.2$; **11b**: $\times 1$, JUE no. 15669-1; **12a-b**: $\times 1$, JUE no. 15669-2; Loc. Korf Bay, Russia, Ejobyi Horizon. **14**: *Kaneharaia ausiensis* (Ilyina), $\times 1$, JUE no. 15665-2, topotype, Loc. 2, Ausinskaya F. **10**: *Phacosoma tomikawensis* (Takagi), $\times 1$, JUE no. 15679, Loc. Kakuma, Omma Formation. White arrows in **1**, **3**, **6b**, **11a** show the subumbonal pit.

mens as *Dosinia* (*Kaneharaia*) *rumoensis* Amano [sic]. Our specimens seem to constitute a new species, but poor preservation of the Kamchakta and Kodiak specimens prevents us from establishing a new species.

Allison (1978) and Marinovich and Moriya (1990) only listed *Dosinia* and *D. whitneyi* respectively from the Narrow Cape Formation in Kodiak Island. Judging from the location, we suspect that their specimens are identical with the present species.

Distribution.—Early middle Miocene Ejoviy Horizon, Korf Bay, eastern Kamchatka, Russia; early middle Miocene Narrow Cape Formation, Kodiak Island, Alaska.

Revision of *Kaneharaia*

Dosinia (*Kaneharaia*) *kaneharai ouchiensis* was described by Kanno (1955) from the Miocene Yoshigasawa Formation in Miyagi Prefecture. According to him, this subspecies can be discriminated from *K. kaneharai* (s.s.) by its higher shell. However, the holotype and topotype specimens of *D.(K.) kaneharai ouchiensis* were slightly compressed laterally, judging from Kanno's (1955) figures and topotype specimens stored at IGPS. As mentioned by Masuda (1967), it is sometimes hard to distinguish *D.(K.) kaneharai ouchiensis* from *K. kaneharai* (s.s.). Therefore, there is no reason to follow this separation.

D.(K.) kaneharai fujinensis was established by Masuda (1967) from the Miocene Fujina Formation in Shimane Prefecture. This subspecies was separated from *K. kaneharai* (s.s.) based on an elongated shell. However, the shell outline of *K. kaneharai* (s.s.) in our specimens from the Kanomatazawa Formation shows a wide range of variation from subcircular to elongate ovate shell. The surface of the holotype of *D.(K.) kaneharaia fujinensis* is sculpted by 11 concentric ribs between 10 mm and 20 mm from the beak just the same as in *K. kaneharai* (s.s.). For the above reasons, we also do not accept the separation of *D.(K.) kaneharaia fujinensis* from *K. kaneharai kaneharai* (s.s.).

Evolutionary history of *Kaneharaia*

To sum up the discussion above, the genus *Kaneharaia* consists of four species in the North Pacific region, : *K. kaneharai* (Yokoyama)(middle-late Miocene), *K. kannoi* (Masuda) (early middle Miocene), *K. ausiensis* (Ilyina) (early middle Miocene-early Pliocene) and *K. sp.* (early middle Miocene). Moreover, as described above, the Astoria species of "*Dosinia*" and "*D. mathewsonii*" most probably belong to the genus *Kaneharaia*.

There is no Oligocene record of *Kaneharaia* in the northwestern Pacific region. On the other hand, one species most probably included in *Kaneharaia* and two species of *Dosinia* have been reported from the upper Oligocene of northwest and central America. "*Dosinia*" *mathewsonii* from the upper Oligocene of California is most probably a *Kaneharaia* as discussed above. Woodring (1982) recorded *D. aff. delicatissima* Brown and Pilsbry, 1913 from the upper Oligocene Bohio Formation of Panama. On the Atlantic coast, Palmer (1927) illustrated *D. chipolana* Dall, 1903 from

the Oligocene Silex beds of Florida.

Taking the phylogenetic relationship and fossil records into consideration, *Kaneharaia* first appeared in the north-eastern Pacific during the late Oligocene.

Among the northwestern Pacific species, *K. kannoi* is confined to the early middle Miocene in northeastern Honshu and North Korea while *K. kaneharai* might be directly derived from *K. kannoi* and occurs from the middle to late Miocene in Honshu (Figure 5). *K. ausiensis* is related to *K. kannoi* and first appeared in the early middle Miocene in Sakhalin and Hokkaido. This species also occurs in the early Pliocene of Hokkaido and central Honshu. *K. sp.* is locally restricted to eastern Kamchatka and Kodiak Island in the early middle Miocene. From the early middle Miocene Astoria Formation in Oregon, *Kaneharaia*-like species have been reported.

Judging from the above distribution, *Kaneharaia* migrated to the northwestern Pacific region during the early middle Miocene time, corresponding to the Neogene Climatic Optimum. Thus, *Kaneharaia* represents another example of a mollusc that shows westward spreading in the North Pacific and is an exceptional in being an extinct genus among this group.

When she discussed the evolution of *Mercenaria* Schumacher, 1817, Harte (1998) pointed out that all Japanese "*Mercenaria*" should be placed in *Securella* Parker, 1949 because



Figure 5. Distribution of *Kaneharaia*.

they lack a rugose nymph. According to her, *Mercenaria* arose from the early Oligocene *S. mississippiensis* during the late Oligocene. *Securella* first appeared in the northeastern Pacific in the late Oligocene while the oldest record of *Securella* in the northwestern Pacific date from the Miocene (Harte, 1998). Such an evolutionary pattern is very similar to that of *Kaneharaia* and *Dosinia*. It is reasonable to conclude that both genera have a common ancestor. Then, after the late Oligocene, *Kaneharaia* flourished in the North Pacific region like *Securella*. On the other hand, *Dosinia* radiated in the Atlantic coast region like *Mercenaria*.

Besides *Kaneharaia* and *Securella*, Amano (1998) listed *Compsomyx* (Veneridae) as another example of a westward-spreading group. More examples of this type of migration will no doubt be found in other venerids.

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A new Foraminifera from the upper Middle Eocene of the Ebro Basin, Spain

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Abstract. *Serraia cataloniensis* gen. et sp. nov. is differentiated from other pellatispiracean Foraminifera by the presence of one or more intercalary whorls of median chambers winding in the same direction as the primary whorl, and by frequent protoconchal and deуроconchal diverticula and a short spire of chambers around the deуроconch. *S. cataloniensis* is described from the La Tossa Formation of the Bartonian regressive cycle of sedimentation in the Ebro Basin, Barcelona region, Spain.

Key words: Bartonian regressive cycle, Ebro Basin, La Tossa Formation, Late Bartonian, *Serraia cataloniensis*, Spain

Introduction

At the second meeting of the IGCP 393, "Neritic Events at the Middle-Upper Eocene Boundary", in Vic, Spain, 2–6 September 1997, the field trip guided by Serra-Kiel *et al.* (1997) took us to different outcrops of Lutetian and Bartonian sediments in the Ebro Basin, southeastern Pyrenean Foreland Basin, Catalonia, Spain. The Puig Aguilera outcrop lies at 41°35'N. Lat. 1°39'E. Long., on the Puig Aguilera, a mountain 5 km northeast of the town of Igualada, 50 km northwest of Barcelona (Figure 1). The geologic section in the Puig Aguilera outcrop (Serra-Kiel *et al.*, 1997, p. 43, fig. 38; Figure 1) begins with marls alternating with sandstone beds in the lower sequence. Above this sequence, there is an interval of marls and sandstones alternating with limestone beds. Serra-Kiel *et al.* (1997) interpret the former as belonging to the upper part of the Bartonian transgressive facies of the La Tossa Formation (Ferrer, 1971), while the latter belongs to the Bartonian regressive facies of the same formation. Sample 4 at the Puig Aguilera outcrop is from the marls corresponding to the Bartonian regressive facies and is rich in larger foraminifers. Especially common are *Asterocyclina stellaris* (Brunner, 1848 MS., in Rüttimeyer, 1850), *Discocyclina pratti* (Michelin, 1946), *D. sella* (d'Archiac, 1850), *Heterostegina reticulata* Rüttimeyer, 1850, *Operculina schwageri* Silvestri, 1928, *Pellatispira madaraszii* (Hantken, 1875), *Orbitoclypeus* sp., and *Nummulites* sp.

The regressive facies of the Bartonian cycle occurs in the Igualada and Vic areas, eastern Ebro Basin, Barcelona region, and changes laterally. The facies of the La Tossa Formation in the Igualada area is correlated to the Saint Marti Xic Limestone Formation (Reguant, 1967) represented by deltaic and reef sediments in the Vic area. On top of the deltaic-reef complex of the Bartonian regressive cycle and

below the evaporitic sediments of the Cardona Formation (Riba, 1975) in the Igualada and Vic areas, there is a Terminal Complex, named by Trave (1992), which reflects the change from marine to continental sedimentation. The Terminal Complex corresponds to the magnetostratigraphic scale from 17.2 to 17.1, and to planktonic foraminiferal Zone P.15 of Berggren *et al.* (1995). Thus the age of the Bartonian regressive facies of the Bartonian marine sediments in the Igualada and Vic areas is regarded as Late Bartonian.

One of the major achievements of project IGCP 393 was the identification of additional larger foraminifers. *Serraia cataloniensis* gen. et sp. nov. occurs in marls in sample 4, which Dr. Serra-Kiel kindly sent to the author for study, and is found there in association with *Biplanispira mirabilis* (Umbgrove, 1937) and the foraminifers listed above.

Systematic paleontology

Order Foraminiferida

Suborder Rotaliina

Superfamily Nummulitacea

Family Pellatispiridae Hanzawa, 1937

Remarks.—In addition to the type genus, Matsumaru (1996a, p. 110–118) assigned the genus *Biplanispira* Umbgrove, 1937 to the family Pellatispiridae Hanzawa, 1937, because of its characteristic planispiral to low trochospiral coiling, sub-sutural and intraseptal radial canals, vertical canals or fissures, and no marginal cord, following Loeblich and Tappan's (1987) classification. Also Matsumaru (1996a) emended the diagnosis of the family such that the secondary and surface chambers are differentiated from the spiral and umbilical sides of the test. Moreover Matsumaru (1996b) transferred the genus *Bolkarina* Sirel, 1981 to the family

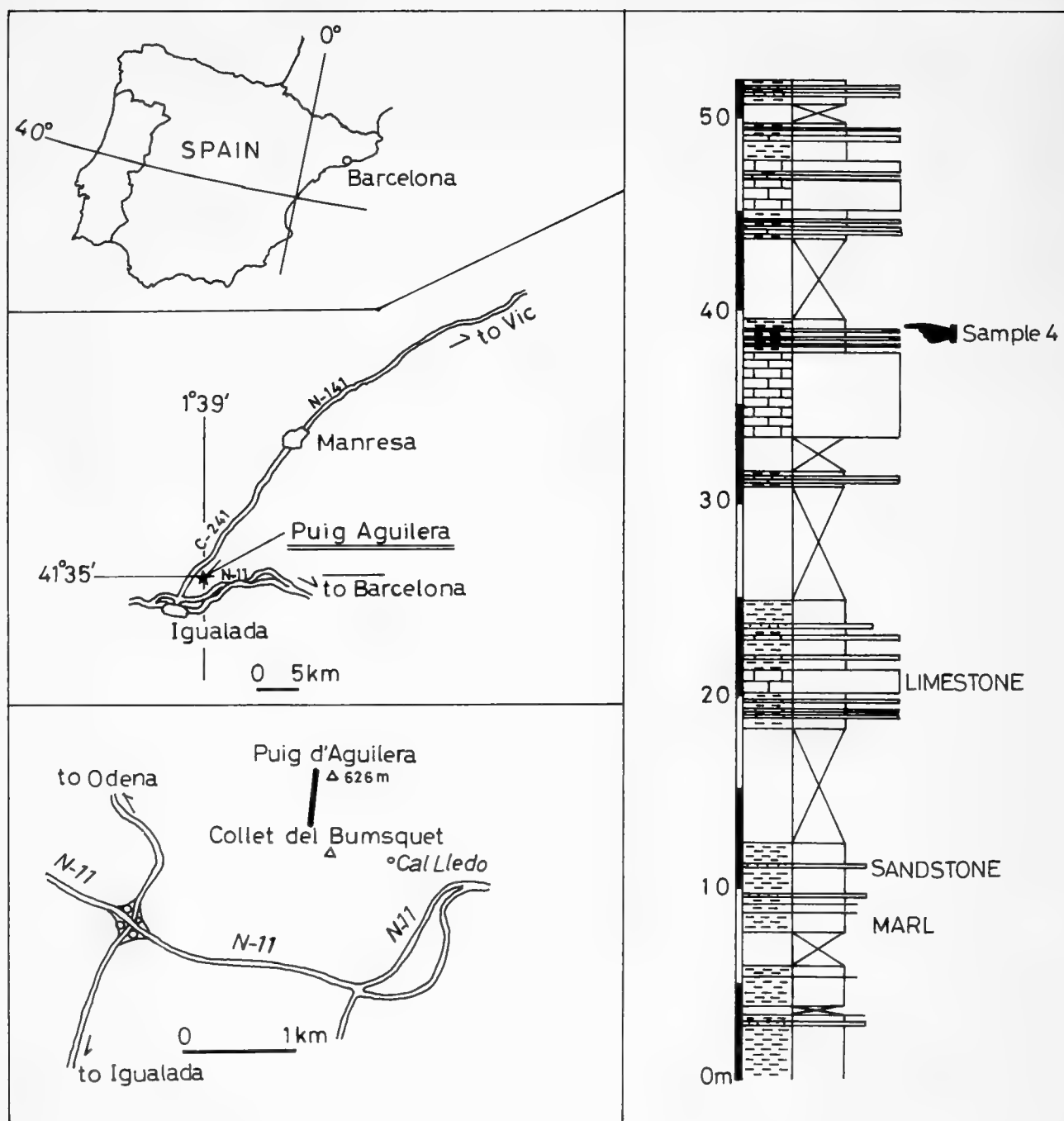


Figure 1. Geographic and stratigraphic position of sample locality (sample 4) from Puig Aguilera outcrop, Igualada City, northwest of Barcelona, Spain.

Discocyclinidae Galloway, 1928 from the family Pellatispiridae.

Genus *Serraia* gen. nov.

Type species.—*Serraia cataloniensis* sp. nov.

Diagnosis.—A pellatispiriid genus characterized by remarkable development of secondary and tertiary spiral chambers of intercalary whorls in early growth stage of planispiral to low trochospiral whorl of primary spiral chambers, and by frequent presence of protoconchal and deuterococonchal diverticula and short spiral chambers around deuterococonch.

Description.—Test lenticula, bilaterally symmetrical in outline with granules extending to pillars distributed rather spirally over surface of test; bilocular embryo of protoconch and deuterococonch frequently containing protoconchal and deuterococonchal diverticula, and a short spire of small chambers around deuterococonch, followed by a primary coil of loosely evolute, later becoming involute whorls of large spiral chambers (i. e. primary spiral chambers), together with secondary and tertiary intercalary whorls of small spiral chambers (i. e. secondary and tertiary spiral chambers) added between whorls of primary coil; all chambers connected by a basal foramen with intraseptal, subsutural and rather canals, winding in same direction as primary whorls towards periphery of test; later primary spiral chambers subdivided into irregularly arranged spiral chambers at peripheral part of test as seen in *Biplanispira*. Lateral layers thickest at center and gradually attenuated towards periphery of test, pierced by numerous vertical pores opening between numerous pillars embedded in lateral layers, and by numerous vertical and radial canals; vertical pores opening covered by thin and finely cribrate roofs of small surface chambers. Test wall calcareous, thick, fibrous and lamellar with two layers of fibrous structure, inner one thin and compact, and outer one

thick and coarsely perforate.

Etymology.—The genus name is after Dr. Josep Serra-Kiel, who provided the pellatispiracean-bearing sample in this study.

Stratigraphic horizon.—Upper part of the La Tossa Formation.

Comparison.—The present genus resembles the genus *Biplanispira* Umbgrove by the presence of a single median layer of primary spiral chambers, and later bifurcating layers of spirally disposed chambers. However, *Serraia* is distinguished from *Biplanispira* in having the second and third median layers of chambers developed from the third and fourth chambers of the primary spiral chambers, respectively, which wind in the same direction as the primary whorl, and also in having frequent protoconchal and deuterococonchal diverticula and a short single layer of chambers around the deuterococonch. *Serraia* resembles *Dictyoconoides* Nuttall, 1925 and *Dictyokathina* Smout, 1954 in having median chambers formed by repeated doubling (originated from bilocular embryonic and median chambers) and in having a test wall with fibrous, lamellar structure that is pierced by vertical canals. However, this new genus is distinguished from them in having double median chambers originated from the primary spiral chambers in an early nepionic stage, in having median layers of fibrous structure, and in lacking an umbilical mass of numerous pillars. Moreover, *Serraia* is distinguished from the genus *Boninella* Matsumaru, 1996a in having chamber layers with fibrous and lamellar structure.

Serraia cataloniensis sp. nov.

Figures 2-1-3; 3-1-5; 4-1-3; 5-1-3

Material.—Holotype: a megalospheric specimen in a half test, Saitama University coll. no. 8841 (Figures 2-1; 3-1); Paratype: equatorial sections of megalospheric specimens, Saitama University coll. no. 8842 (Figures 2-2; 3-5), Saitama

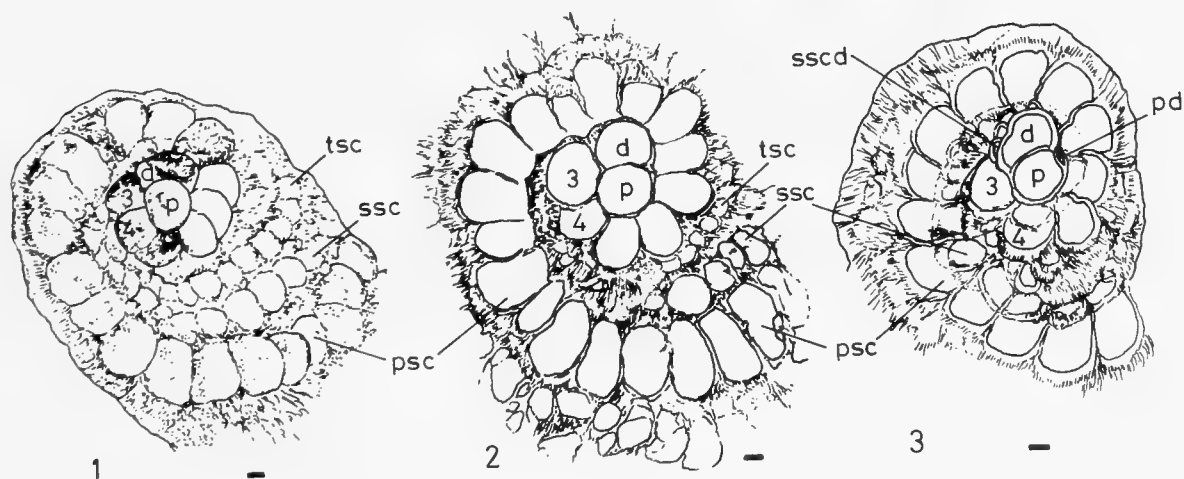
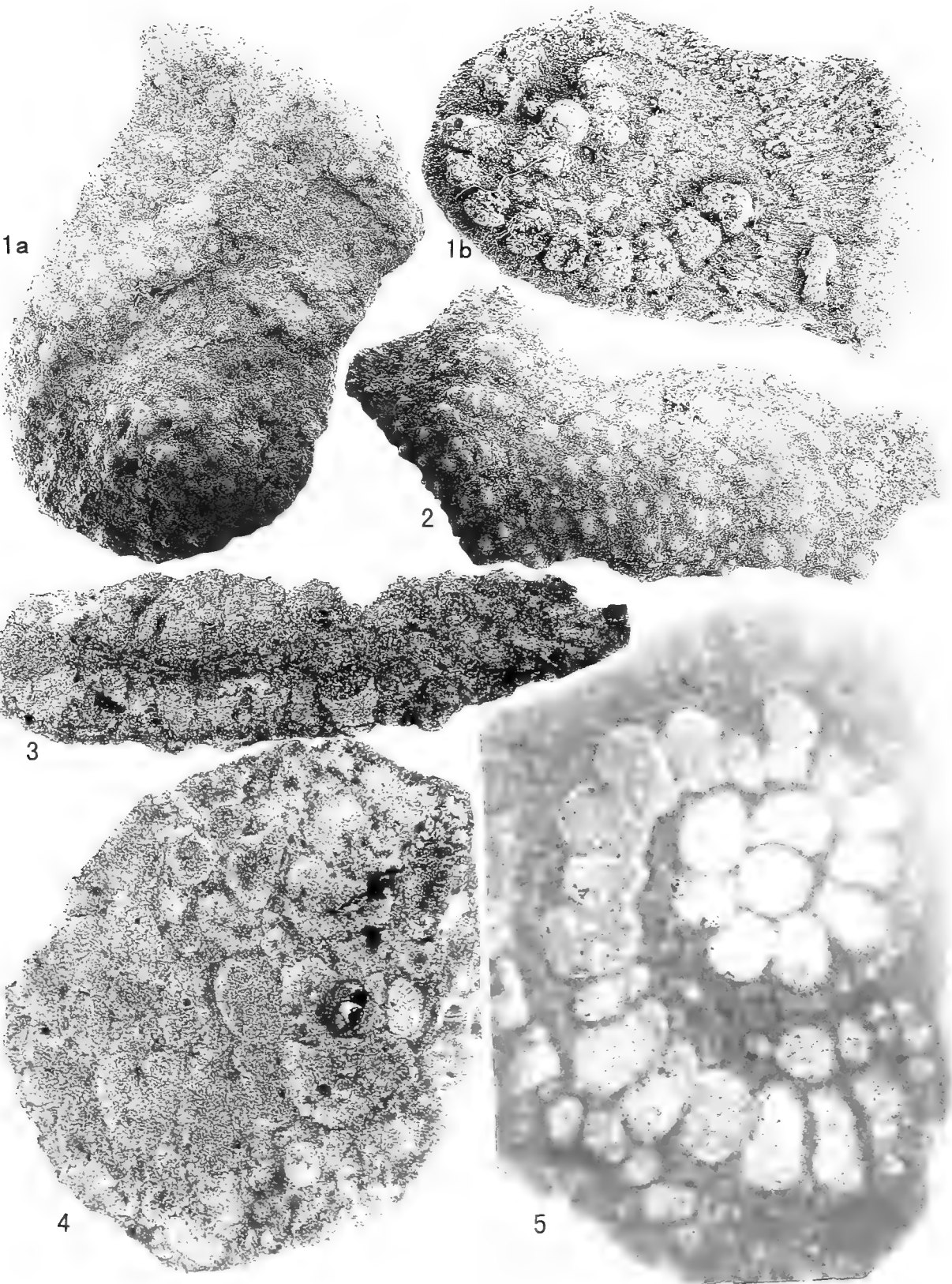


Figure 2. *Serraia cataloniensis* gen. et sp. nov. Drawings of megalospheric specimens. 1. Holotype, Saitama University coll. no. 8841 (see also Figure 3-1). 2. Paratype (see also Figure 3-5), Saitama University coll. no. 8842. 3. Paratype (see also Figure 5-2), Saitama University coll. no. 8843. Abbreviations: p=protoconch; pd=protoconchal diverticulum; d=deuterococonch; 3,4=third and fourth primary spiral chambers; psc=primary spiral chambers; ssc=secondary spiral chambers; tsc=tertiary spiral chambers; sscd=short spiral chambers around deuterococonch. Scale bars=100 μ m.



University coll. no. 8843 (Figures 2-3; 5-2), Saitama University coll. no. 8846 (Figure 5-1), Saitama University coll. no. 8847 (Figures 5-3a-b), and Saitama University coll. no. 8850 (Figure 3-4); Paratype: test surface and/or equatorial views of megalospheric or microspheric specimens, Saitama University coll. no. 8844 (Figures 4-1a-c), Saitama University coll. no. 8845 (Figures 4-2a-b), Saitama University coll. no. 8848 (Figure 3-2) and Saitama University coll. no. 8851 (Figures 4-3a-b); Paratype: vertical sections of megalospheric specimens, Saitama University coll. no. 8849 (Figure 3-3).

Description.—Test thin (0.6 to 0.9 mm in thickness), lenticular (2.0 to 4.0 mm in diameter) with rather thick marginal periphery; form ratio (diameter/thickness) 4.0 to 7.7 in megalospheric form; and 9.0 in single microspheric form observed which is 4.5 mm in diameter. Megalospheric embryonic chambers biloculine; subspherical to spherical protoconch ranging from 160×140 to $370 \times 370 \mu\text{m}$ in diameter in seven specimens, and reniform deutoconch 200×160 to $430 \times 370 \mu\text{m}$ in diameter in seven specimens; whole embryonic chambers 320 to $600 \mu\text{m}$ in diameter across both protoconch and deutoconch in seven specimens; outer wall of embryonic chambers 20 to $30 \mu\text{m}$ thick in seven specimens; third primary spiral chamber 100×120 to $265 \times 350 \mu\text{m}$ in radial and tangential diameters in seven specimens; and fourth primary spiral chamber 60×120 to $240 \times 215 \mu\text{m}$ in radial and tangential diameters in seven specimens. Other primary spiral chambers developed into a planispirally to low trochospirally evolute whorl in mature stage and into involute whorl in gerontic stage; first whorl divided by septa into 7 to 10 chambers, first whorl and a half with 15 to 20 chambers, and second whorl with 25 ? to 33 ? chambers in seven specimens. Secondary spiral chambers of second median layer in planispiral to low trochospiral whorl 60×100 to $220 \times 240 \mu\text{m}$ in maximum radial and tangential diameters in seven specimens. Tertiary spiral chambers of third median layer in planispiral to low trochospiral whorl 100×200 to $200 \times 130 \mu\text{m}$ in maximum radial and tangential diameters in five specimens; both secondary and tertiary spiral chambers wind in same direction as primary spiral chambers. Median layer of primary spiral chambers subdivided into irregularly arranged, spiral chamber layers towards periphery. Protoconchal diverticula arcuate, 28×42 to $30 \times 62 \mu\text{m}$ in radial and tangential diameters in three specimens, and deutoconchal diverticula arcuate $80 ? \times 140 ? \mu\text{m}$ and $83 \times 145 \mu\text{m}$ in radial and

tangential diameters in two specimens. Short spiral chambers around deutoconch frequently present and arcuate, 25×62 to $40 \times 93 \mu\text{m}$ in maximum radial and tangential diameters in two specimens. Lateral layers thickest at center and attenuated towards periphery of test, and pierced by numerous open pores or vertical canals of 8 to $20 \mu\text{m}$ diameter. Pore openings covered by thin roofs of small surface chambers with 135×38 to $145 \times 40 \mu\text{m}$ in maximum tangential diameter and height in three specimens. Test wall thick, fibrous, and perforate; canal system showing radial, simple and marginal, and intraseptal canal present. Dorsal and umbilical pillars present over lateral walls; smaller ones 85 to $100 \mu\text{m}$ in diameter, and larger ones 135 to $185 \mu\text{m}$ in diameter. Aperture with longitudinal grooves on base of apertural face; in present material, measurements of seven megalospheric forms given in Table 1.

Etymology.—The species name is derived from the province of Catalonia, Spain.

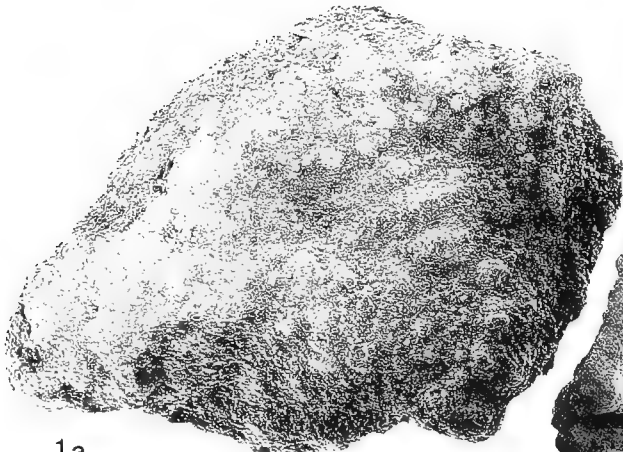
Type locality.—Sample locality (Sample 4) of Puig Aguilera outcrop, Igualada, 50 km northwest of Barcelona, Spain (Figure 1).

Remarks.—*Serraia cataloniensis* sp. nov. resembles *Biplanospira mirabilis* (Umbgrove, 1936), but is easily distinguished from the latter in having the secondary and tertiary spiral chambers developed in the same direction as the primary spiral chambers, and in possessing frequent protoconchal and deutoconchal diverticula and short spiral chambers around the deutoconch. The author considers that this new species may have evolved from *Biplanospira mirabilis* (Umbgrove) by developing secondary and tertiary spiral chambers directly from the spiral chambers.

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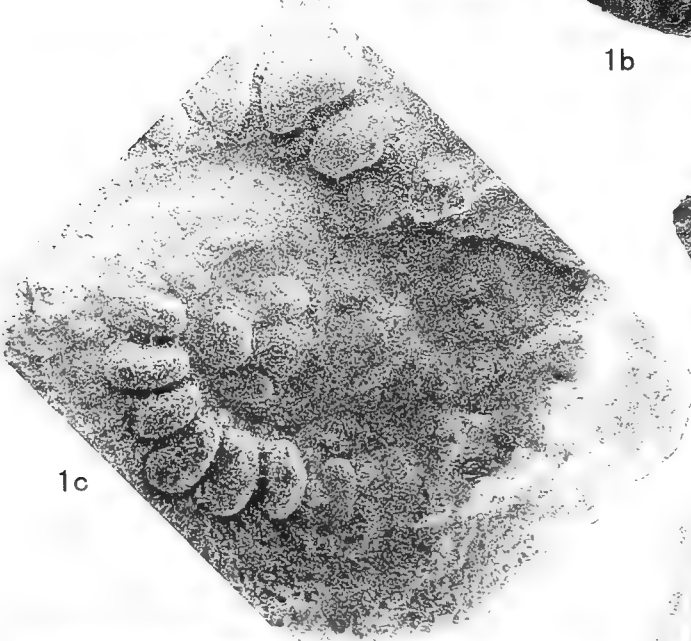
— **Figure 3.** *Serraia cataloniensis* gen. et sp. nov. **1a.** External view (spiral side) of megalospheric specimen (holotype), showing large- and small-sized granules, and rather thick marginal periphery of test. **1b.** Equatorial and internal view of holotype showing embryonic chambers with half-broken deutoconch; primary spiral chambers with 5th, 9th and 12th broken chambers, and secondary and tertiary spiral chambers, all coiling in same direction except for peripheral chambers. $\times 26$. **2.** External view of spiral side of test in microspheric specimen, paratype, Saitama University coll. no. 8848, $\times 22$. **3.** Vertical section of megalospheric specimen, paratype, Saitama University coll. no. 8849, showing spiral and surface chambers, lateral layers thickest at center and attenuated towards periphery, large and small pillars, pore openings, and canals, $\times 43$. **4.** Equatorial section of broken specimen, paratype, Saitama University coll. no. 8850, showing irregularly arranged primary spiral chambers towards periphery of test, coiling opposite direction to primary whorl as seen in *Biplanospira*, and also coiling in same direction as primary whorl, $\times 43$. **5.** Equatorial section of megalospheric specimen, paratype, Saitama University coll. no. 8842, showing embryonic chambers, primary spiral chambers, and secondary and tertiary spiral chambers, all coiling in same direction, $\times 40$.



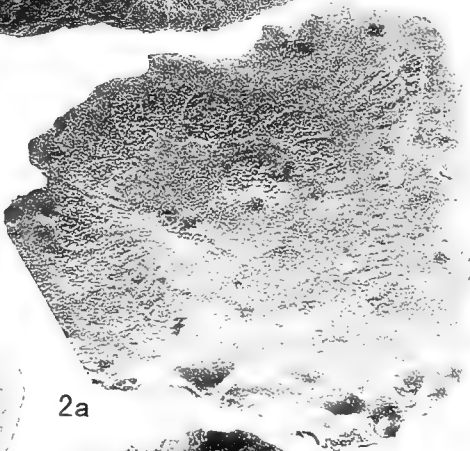
1a



1b



1c



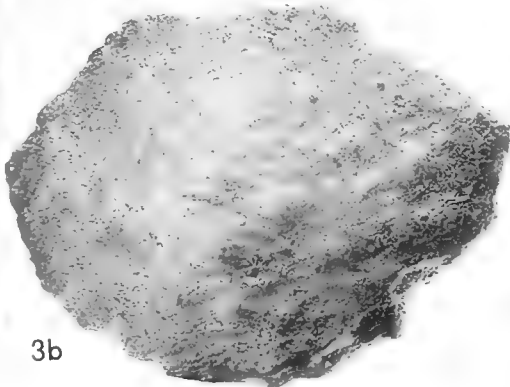
2a



2b



3a

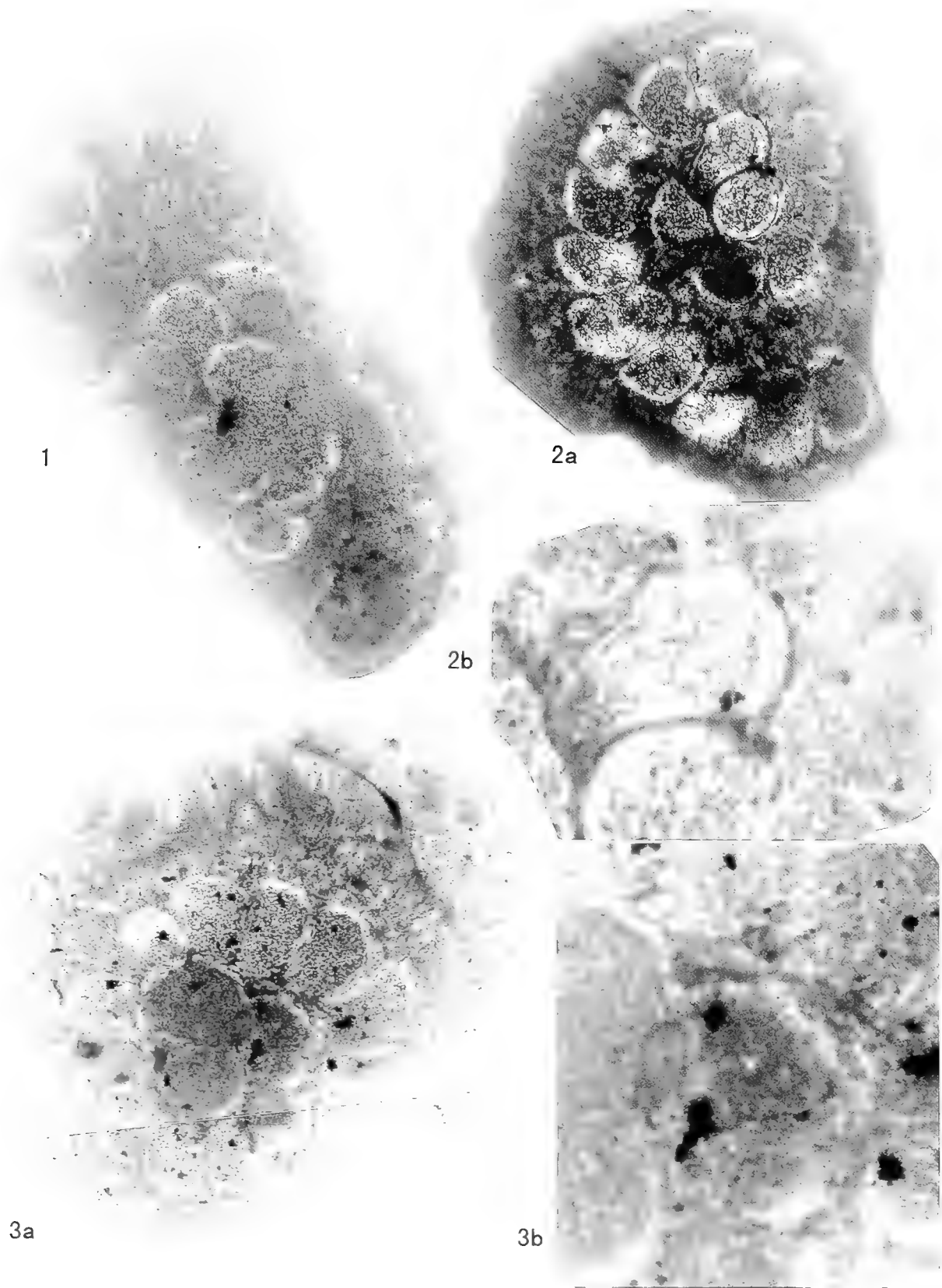


3b

Table 1. Measurements of internal equatorial view and equatorial sections of *Serraia cataloniensis* sp. nov.

| Specimen | Holotype no. 8841 (Fig. 3-1) | Paratype no. 8842 (Fig. 3-5) | Paratype no. 8843 (Fig. 5-2) | Paratype no. 8846 (Fig. 5-1) | Paratype no. 8847 (Fig. 5-3) | Paratype no. 8844 (Fig. 4-1) | Paratype no. 8845 (Fig. 4-2) |
|--|------------------------------------|------------------------------------|------------------------------------|------------------------------------|------------------------------------|------------------------------------|------------------------------------|
| Diameter (mm) | 3.6 | 3.1 | 2.3 | 3.0 | 3.0 | 4.0 | 2.0 |
| Thickness (mm) | 0.9 | 0.6 | 0.3 | 0.4 | 0.5 | 0.9 | 0.3 |
| Form ratio (diameter/thickness) | 4.0 | 5.2 | 7.7 | 7.5 | 6.0 | 4.4 | 6.7 |
| Embryonic chambers | | | | | | | |
| protoconch diameter (μm) | 370×370 | 350×290 | 302×272 | 235×265 | 360×250 | 220×140 | 160×140 |
| deuteroconch diameter (μm) | 374×212 | 320×208 | 350×230 | 235×170 | 430×340 | 220×160 | 200×160 |
| distance across both chambers (μm) | 600 | 498 | 502 | 435 | 600 | 320 | 320 |
| wall thickness (μm) | 30 | 30 | 20 | 28 | 30 | 28 | 22 |
| Protoconchal diverticula | | | | | | | |
| radial diameter (μm) | | | 30 | 30 | 28 | | |
| tangential diameter (μm) | | | 62 | 42 | 42 | | |
| Deuteroconchal diverticula | | | | | | | |
| radial diameter (μm) | | | | 80 ? | 83 | | |
| tangential diameter (μm) | | | | 140 ? | 145 | | |
| Spiral chambers around deuteroconch | | | | | | | |
| radial diameter (μm) | | | 33 40 40 | | 25 33 | | |
| tangential diameter (μm) | | | 72 52 93 | | 62 40 | | |
| Primary spiral chambers | | | | | | | |
| Third chamber | | | | | | | |
| radial diameter (μm) | 145 | 265 | 208 | 100 | 220 | 135 | 100 |
| tangential diameter (μm) | 280 | 350 | 290 | 140 | 290 | 165 | 120 |
| Fourth chamber | | | | | | | |
| radial diameter (μm) | 200 | 165 | 240 | 140 | 180 | 60 | 80 |
| tangential diameter (μm) | 160 | 145 | 215 | 140 | 220 | 120 | 110 |
| number in 1st whorl | 8 | 8 | 7 | 9 | 10 | 7 | 9 |
| number in 1+1/2 whorl | 16 | 18 | 15 | 17 | 18 | 15 | 18 |
| number in 2nd whorl | 30? | 33? | 28? | 29 | 29? | 29 | 25? |
| Secondary spiral chambers | | | | | | | |
| radial diameter (μm) | 230 | 220 | 230 | 190 | 140 | 60 | 60 |
| tangential diameter (μm) | 160 | 240 | 230 | 200 | 186 | 100 | 100 |
| Tertiary spiral chambers | | | | | | | |
| radial diameter (μm) | 200 | 120 | 100 | 100 | | 100 | |
| tangential diameter (μm) | 130 | 95 | 200 | 200 | | 200 | |

← **Figure 4.** *Serraia cataloniensis* gen. et sp. nov. **1a.** External view of megalospheric specimen, paratype, Saitama University coll. no. 8844, in umbilical side of test, showing dextral distribution of large- and small-sized granules. **1b.** Equatorial and internal view of same specimen of Figure 4-1a, showing embryonic chambers, and primary, secondary and tertiary spiral chambers, all coiling in sinistral direction, $\times 26$. **1c.** Central part of internal view of Figure 4-1b, showing embryonic and primary spiral chambers, and secondary and tertiary spiral chambers, $\times 43$. **2a.** Equatorial and internal view of megalospheric specimen, paratype, Saitama University coll. no. 8845, $\times 43$. **2b.** Central part of internal view in Figure 4-2a, showing embryonic and primary spiral chambers, and secondary spiral chambers connected by intraseptal, subsutural and radial canals from third chamber and 7th chamber of primary spiral chambers, $\times 107$. **3a.** External view of megalospheric specimen, paratype, Saitama University coll. no. 8851, showing spiral side of test. **3b.** External view of same specimen as Figure 4-3a showing umbilical side of test, $\times 26$.



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← **Figure 5.** *Serraia cataloniensis* gen. et sp. nov. **1.** Equatorial section of megalospheric specimen, paratype, Saitama University coll. no. 8846, showing embryonic chambers, primary spiral chambers, and secondary and tertiary spiral chambers, all coiling in same direction, $\times 43$. **2a.** Equatorial section of megalospheric specimen, paratype, Saitama University coll. no. 8843, showing embryonic and primary spiral chambers, secondary spiral chambers, protoconchal diverticulum, and short spiral chambers arranged deutoconch, $\times 43$. **2b.** Central part of equatorial section in Figure 5-2a, showing protoconchal diverticulum and short spiral chambers around deutoconch connected by deutoconchal stolons and probably intraseptal, subsutural and radial canals from third chamber, $\times 107$. **3a.** Equatorial section of megalospheric specimen, paratype, Saitama University coll. no. 8847, showing embryonic, primary and secondary spiral chambers, deutoconchal diverticulum, and short spiral chambers around deutoconch, $\times 43$. **3b.** Central part of equatorial section in Figure 5-3a, showing deutoconchal diverticulum, and short spiral chambers connected by deutoconchal stolons and intraseptal, subsutural and radial canals or stolons? $\times 95$.

The Late Bathonian gastropod fauna of Kutch, western India—a new assemblage

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Abstract. The Middle Jurassic sediments of Kutch have been known all over the world as a veritable storehouse of diverse fauna, particularly ammonites. The present investigation has brought to light a rich haul of gastropods hitherto unknown in Kutch. The present assemblage includes eleven new species belonging to nine genera. They are: *Colpomphalus jumarensis* sp. nov.; *Emarginula karuna* sp. nov.; *Helicacanthus chanda* sp. nov.; *Riselloidea tagorei* sp. nov.; *R. elongata* sp. nov.; *Onkospira kutchensis* sp. nov.; *Proconulus jadavpuriensis* sp. nov.; *Neritopsis (Neritopsis) patchamensis* sp. nov.; *N. (Hayamiella) sankhamala* sp. nov.; *Hayamia mitra* sp. nov. and *Globularia spathi* sp. nov.

The assemblage shows strong Tethyan affinity at generic level, but species display marked endemism since Kutch belongs to a distinct Indo Madagascan Faunal Province. The present finding refines and widens the spatiotemporal distribution of these genera.

Key words: Gastropoda, Kutch, Middle Jurassic, systematics, western India

Introduction

The marine Jurassic sediments of Kutch were deposited in a newly emerging basin that developed as an extension of the Tethys during separation of Africa and India consequent to the rifting of the Gondwana Superplate (Biswas, 1982, 1991). The Jurassic rocks yield many diverse shallow marine taxa. The fossils are numerous and remarkably well preserved. Amongst them the ammonites attract the most attention of palaeontologists. Among the ammonites many are time-diagnostic forms that provide finer time resolution and help in establishing regional standard biozonations and inter-continental correlation with Europe and other areas. The faunal horizons that yield gastropods, may be assigned to an age ranging from the Late Bathonian to Tithonian.

Many classic studies on this biota, e.g., Cephalopoda (Waagen, 1873–75; Spath, 1927–33), Bivalvia (Kitchin, 1900; Cox, 1940, 1952), Brachiopoda (Kitchin, 1900) and corals (Gregory, 1893, 1900) were made by great masters of the last and this centuries. It is rather surprising that the vast gastropod fauna from the different sections of the mainland and 'islands' of Kutch escaped their notice, notwithstanding the scanty reports of a few gastropod species (Maithani, 1967; Mitra and Ghosh, 1979).

In this present endeavour, we describe 11 new species of the Bathonian, some of which continue to the base of the Middle Callovian. The present study covers a large number

of specimens systematically collected in the field with a precise stratigraphic background by us and other members of the Palaeontological Laboratory, Department of Geological Sciences, Jadavpur University.

These species belong to nine genera of seven families. They are *Colpomphalus jumarensis* sp. nov.; *Emarginula karuna* sp. nov.; *Helicacanthus chanda* sp. nov.; *Riselloidea tagorei* sp. nov.; *R. elongata* sp. nov.; *Onkospira kutchensis* sp. nov.; *Proconulus jadavpuriensis* sp. nov.; *Neritopsis (Neritopsis) patchamensis* sp. nov.; *N. (Hayamiella) sankhamala* sp. nov.; *Hayamia mitra* sp. nov.; and *Globularia spathi* sp. nov. They show strong Tethyan affinity at generic level, especially with Europe (see Knight *et al.*, 1960). Biogeographic distributions of the other Kutch biota suggest prevalence of faunal migrational pathways across the Tethys particularly with Europe (Hallam, 1982; Krishna and Cariou, 1990; Kayal and Bardhan, 1998). The faunas are, however, marked by strong provincialism at species level. The sediments developed due to repeated marine transgression–regression cycles in a basin that emerged from the breakup of Gondwana Superland and was surrounded by East Africa, Madagascar and western India (see also Fürsich *et al.*, 1991). This newly formed basin acted as the Eden of evolution for many immigrant faunas that invaded it (Dutta *et al.*, 1996). Rapid diversification of various taxa marks a strong endemism of fauna which constitutes what is called the Indo–Madagascan or Ethiopian Faunal Province. This record of

new taxa widens our knowledge about spatiotemporal distribution of the Jurassic gastropod fauna, which are less comprehensively known and poorly documented in the existing literature.

It should be noted here that recent advances in the studies of suprageneric classification of gastropods have drawn attention to some lacunae in the earlier traditional classifications (e.g. Wenz, 1938–44; Knight *et al.*, 1960). Many higher taxonomic categories are now considered to be paraphyletic, e.g., the Archaeogastropoda (e.g. Hickman and McLean, 1990), and poorly delineated. Major revisionary works are now available for many important groups including their extinct taxa, e.g., on Naticidae and Trochidae (see Kabat, 1991; Hickman and McLean, 1990). Some new schemes have deployed cladistic methodology emphasising the role of derived (apomorphic) conditions and included large character sets. But excessive weight has been given to the characters related to soft parts. The systematic position of many extinct lineages remain still problematic since shell characters may be convergent (Hickman and McLean, 1990). Thus a large amount of uncertainty still prevails in respect of the classification of fossil gastropods. Under such circumstances our endeavour has been to largely retain the general framework (subordinal level and above) of classification given in the Treatise on Invertebrate Paleontology (Knight *et al.*, 1960) while effecting some family or subfamily level changes with regard to certain Kutch taxa in the light of modern classification. In this context the following brief discussion would clarify the taxonomic hierarchies followed in the present study. Particular attention should be drawn to our categorisation of the genera *Riselloidea* and *Onkospira* under the family Trochidae instead of Amberleyidae of the earlier classification and the genus *Helicacanthus* under Turbinidae instead of Nododelphinulidae following Hickman and McLean (1990). Dealing in detail with the shell characters of Amberleyidae, Hickman and McLean (1990) have been very explicit in pointing to the trochid innovations in its shell morphology that are shared with the living species. Of the many trochid subfamilies recognised by them the subfamily Eucyclinae is of particular interest; it covers erstwhile Amberleyidae (Family) and Amberleyinae (Subfamily) and has been divided into three tribes among which the Tribe Eucyclini comprises only the fossil trochids of Middle Triassic to Oligocene age. While discussing this subfamily they have also dealt with those shell characters of the three tribes that separate them from other trochid subfamilies. The historical treatment presented by them clearly demonstrates the weak foundation on which the Amberleyidae of Wenz (1938) and Cox's (*in* Knight *et al.*, 1960) eucycline taxa and superfamily Amberleyacea stand. Similar detailed character analyses that include hard part features have resulted in the placement of erstwhile Nododelphinulidae in the subfamily Angariinae (family Turbinidae) and Proconulinae tentatively under Calliostomatinae (Trochidae) taking into account the assignments which have also been followed here. The scheme used here is logical under rather conflicting positions presently prevailing in fossil gastropod taxonomy and leaves room for more detailed work on an improved, widely acceptable classification.

Stratigraphy

The Mesozoic rocks occupy nearly half of the area in Kutch, covering the mainland as well as three Rann 'islands', and lie nonconformably on the Pre-Cambrian basement (Biswas and Deshpande, 1968). On the mainland the Mesozoic rocks are represented by: Patcham Formation, Chari Formation, Katrol Formation, Bhuj Formation and Deccan Trap in ascending order (for details see Mitra *et al.*, 1979). The thick pile of sediments exceeds more than 3,000 m (Biswas, 1991) and has been regionally folded into three parallel anticlines running northwest-southeast. The Jurassic rocks are best developed in the central anticline (Wynne, 1872; Rajnath, 1932; Poddar, 1959). A set of zones of culmination is observed along the anticlines. These zones of culmination crop out as topographical domes at Jara, Jumara, Nara, Keera etc. (Figure 1) where the inliers of older rocks belonging to the Patcham and Chari Formations mainly occur at the core.

The present gastropod faunas come mainly from the different levels of the Patcham Formation which is partially exposed at Jumara, the locality for the stratotype of the Chari Formation. The Middle Jurassic sediments of the 'islands' belts are included in the formations equivalent to the Patcham Formation and even older ones (Biswas, 1977; Fürsich *et al.*, 1994). Here gastropods occur sporadically, becoming locally abundant at Kuar Bet near Patcham 'island'. The gastropod assemblage of this area appears to be quite distinct from that of Jumara and is dominated mainly by *Katosira* Koken. This level, judged by the associated fauna and stratigraphic position, may represent the Bajocian (see also Fürsich *et al.*, 1994) and these gastropods are therefore not included in the present study.

The exposed sequence of the Patcham Formation at Jumara, which is about 47 m thick, consists of alternations of two distinct lithofacies (Beds 24–26 of Rajnath, 1932; Beds 1–2 of Bardhan *et al.*, 1994) (Figure 2). The lower facies is an alternation between coralline rudstone and cream-coloured

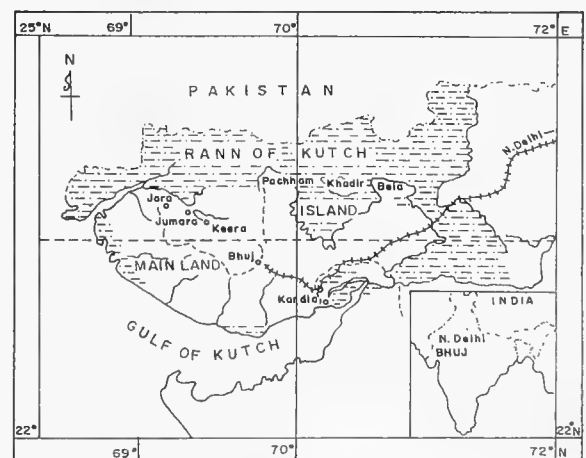
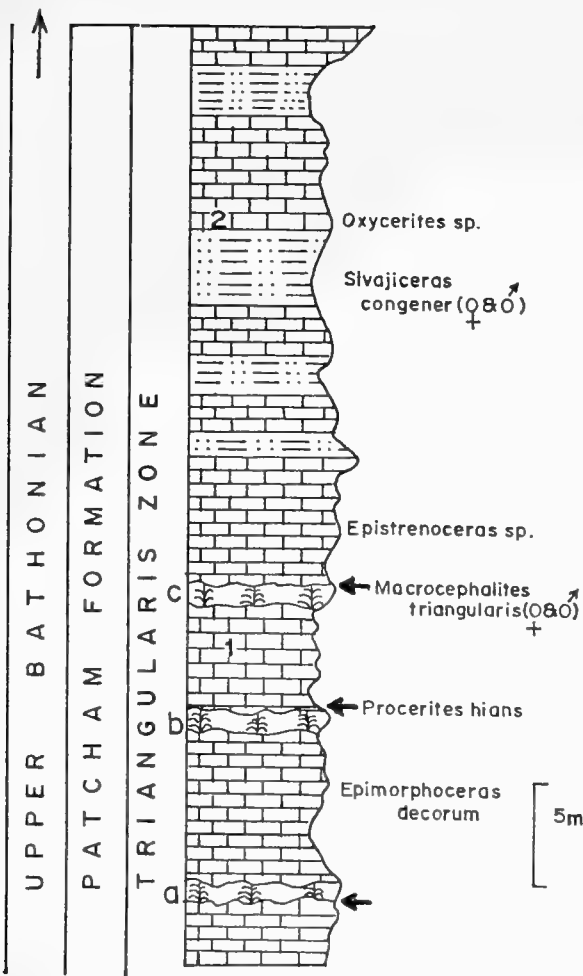


Figure 1. Geographic location of Kutch with Keera and Jumara, the type area of the Chari Formation. The patterned area is the Rann of Kutch.



| Upper Bathonian | | Lower Callovian | Middle Callovian | Age |
|-----------------|----------------|-----------------|------------------|------------------------------|
| Patcham | Chari | | | Formation |
| Triangularis | Chrysolithicus | Formosus | Indosabauda | Reissi |
| | | | | Zone |
| | | | | Species |
| ----- | | | | Proconulus jadavpuriensis |
| ----- | | | | Emarginula karuna |
| ----- | | | | Colpomphalus jumarensis |
| ----- | | | | Neritopsis (N.) patchamensis |
| ----- | | | | Neritopsis (H.) sankhamala |
| ----- | | | | Hayamia mitra |
| ----- | | | | Globularia spathi |
| ----- | | | | Riselloidea tagorei |
| ----- | | | | R. elongata |
| ----- | | | | Onkospira kutchensis |
| ----- | | | | Helicacanthus chanda |

Figure 3. Range chart of different species of gastropods in Kutch. Zones are modified after Dutta (1992).

ammonites belonging to *Procerites* Siemiradzki have been reported from it. This also suggests a late Bathonian age (see also Callomon, 1993; Dutta *et al.*, 1996). Recently, Dutta (1992) made a substantial revision of the standard zonations within the Bathonian–Callovian Stages of Kutch. We follow here the biostratigraphic scheme of Dutta (1992) with modification, and stratigraphic distribution of the present gastropod species is shown in Figure 3 (after Bardhan *et al.*, 1994 with modification).

Systematic Paleontology

All the materials studied are deposited in the Department of Geological Sciences, Jadavpur University, Calcutta, India (JU). Measurements are not provided since specimens are plentiful for most of the species, over three hundred in the case of *Riselloidea tagorei*. These can be provided upon request.

Subclass Prosobranchia
Order Archaeogastropoda
Suborder Macluritina
Superfamily Euomphalacea
Family Helicotomidae
Genus *Colpomphalus* Cossmann, 1916

Type species.—*Straparollus altus* d'Orbigny, 1853; original designation.

wackestone. Biostromes of diverse corals appear at several levels where gastropods are most abundant. The coral biostromes occur in the form of parallel-sided, thin tabular beds. They dominantly consist of largely intact fossils with or without interstitial mud (Dutta *et al.*, 1996). There are large varieties of corals (Gregory, 1900; Pandey and Fürsich, 1993), most of them being in life attitude. Besides corals and gastropods, many other taxa including ammonites also characterise this horizon. The facies is marked by the first appearance of *Macrocephalites* Zittel in Kutch. Judging by its faunal content and a recently found excellent time-diagnostic ammonite, *Epistrenoceras* Bentz (Kayal and Bardhan, 1998), this lower part of the Patcham Formation can safely be assigned to the late Bathonian. The upper facies is, on the other hand, an alternation between cream-coloured wackestone and mud. It supports sparse fauna including gastropods. Only some fragmentary perisphinctid

***Colpomphalus jumarensis* sp. nov.**

Figure 4-1, 2

Material.—Seven specimens. JUM/g 19-22, 594-596. Specimen JUM/g 19 is designated holotype; the rests are paratypes. JUM/g 19-22 were collected from Bed 1, Jumara and JUM/g 594-596 from Bed 2, Keera (see Bardhan *et al.*, 1994).

Diagnosis.—Average-sized *Colpomphalus* (6 to 10 mm high); whorls 4 to 5 in number, gradate with wide sloping concave ramp; ornamentation of three strong spiral carinae, irregularly spaced and middle one relatively weaker, close to first one; prominent collabral ridges prosocline on ramp.

Description.—Shell small in size, maximum height about 10 mm; thick, phaneromphalous; highly depressed and turbiniform with height about half of shell diameter. Apical angle ranges between 120° and 130°. Whorls 4 to 5 in number including protoconch and separated in early stage by weakly grooved suture which becomes conspicuous in later ontogeny. Protoconch poorly preserved, seemingly consists of one and a half smooth, planispiral whorls. Spire very low, conical, obtusely pointed owing to near-planispiral coiling of early whorls. Spire occupies one-fourth of shell height. Body whorl very large, width slightly greater than twice of height; shell rapidly increases in diameter. Whorls gradate with wide sloping ramp, which is concave at upper whorl surface. Outer whorl surface inclined abapically. Body whorl consists of three revolving carinae, which are irregularly spaced. First one situated in ramp margin while third carina at base of whorl forms umbilical border, second carina is close to first. First and third are stronger than second. Umbilical wall steep. Transverse, prosocline ridges fine to sharp, intersect carinae and form pointed tubercles at junctions. Tubercles are variable in number, 20 to 25 on body whorl. Aperture subquadrangular, width of aperture is greater than height. Columellar and basal lips form an angulation at their junction.

Discussion.—Relatively low spire, concave upper whorl surface, tuberculate periphery and angular peristome place the present species securely within the genus *Colpomphalus*. It however, differs from *Colpomphalus exsertus* (Hudleston, 1893) (Knight *et al.*, 1960, fig. 106, 7) from the Bajocian of England mainly in shell ornamentation. *C. exsertus* is ornamented with two revolving carinae and fine collabral threads; conversely, the present species has three strong revolving carinae and strong collabral ridges which are prosocline on ramp. Besides, the present species has fewer whorls and a relatively more protruded spire.

The general shell outline, apertural shape, little raised spire and number of whorls of the present species are comparable with those of the Lower Jurassic (Middle Aalenian) *Colpomphalus baugieri* (d'Orbigny) (1853, p. 307, pl. 321, figs. 13-16) (see also Fischer, 1997, p. 121, pl. 24, figs. 1a-c) of Niort, France. But the European form is stratigraphically older and relatively smaller in size. It is less coarsely ornate and is characterised by numerous fine spiral striae, which are lacking in the present species.

Colpomphalus altus (d'Orbigny) (1853, p. 314, pl. 332, figs.

5-8) (also see Fischer, 1997, p. 124, pl. 22, figs. 5a-c), the type species, is a contemporaneous species from France and is based on a monotypic holotype which is broken and immature and hence comparison is very difficult. Its restored diameter is about 8 mm and thus appears to be smaller. It appears similarly but less strongly ornate, basal ornamentation consisting of numerous striae which are conspicuous by their absence in the Kutch species.

Etymology.—After Jumara area of Kutch, Gujarat, where the species occurs.

Suborder Pleurotomariina

Superfamily Fissurellaceae

Family Fissurellidae

Subfamily Emarginulinae

Genus ***Emarginula*** Lamarck, 1801

Type species.—*Emarginula conica* Lamarck, 1801; original designation.

***Emarginula karuna* sp. nov.**

Figure 4-3-5

Material.—Five specimens. JUM/g 71-75. Specimen JUM/g 71 is designated holotype; the rest are paratypes. Specimens are mostly broken, but their original shells are preserved. All were collected from Bed 1 of Jumara.

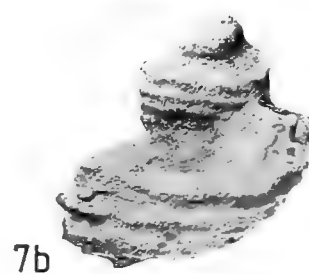
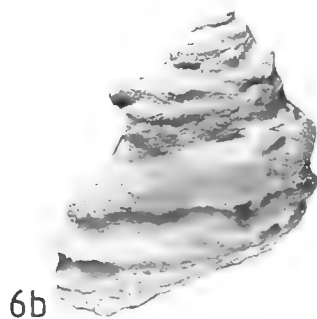
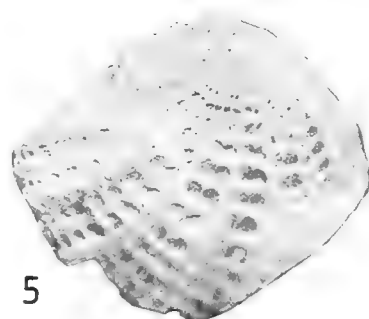
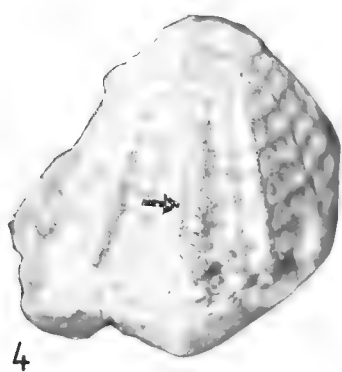
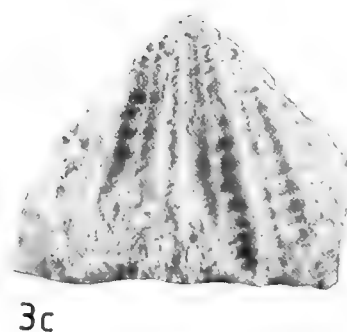
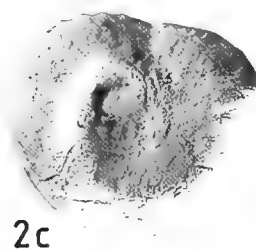
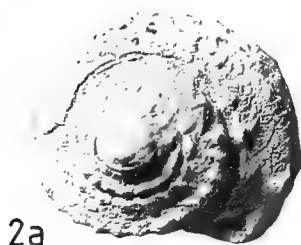
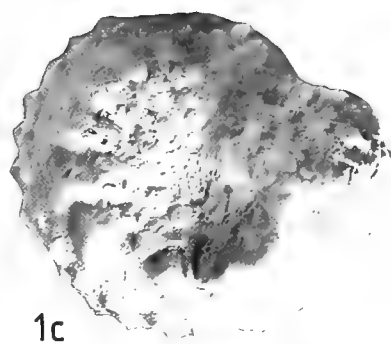
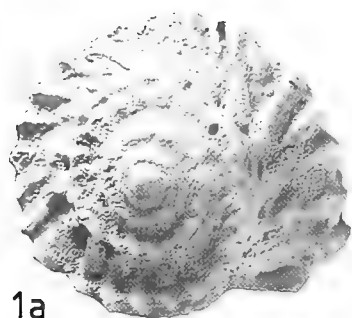
Diagnosis.—Averaged-sized *Emarginula* (8 to 13 mm high); shell short; apex slightly curved; narrow, raised selenizone extending more than three-fourths of shell height from base; in transverse section, shell nearly flattened along selenizone. Shell ornamented with strong, closely spaced axial ribs intersected by relatively weaker spiral cords; weaker axial rib intercalates between two stronger ribs; very fine, dense, transverse and crescent-shaped ribs with concavity towards aperture subdivide selenizone.

Description.—Shell short, maximum height achieved 13 mm; cap-shaped. Apex curved pointing to rear, protoconch missing. Shell convex, slightly flattened along selenizone. Narrow, slightly raised selenizone between two ridges extending more than three-fourths of shell height from base.

Shell ornamented with strong axial ribs intersected by relatively weaker spiral cords resulting in reticulation. Weaker axial rib intercalates between two stronger ribs. This secondary axial rib is similar in strength or may be sometimes weaker than spiral cords. Very fine, dense and transverse ribs subdivide selenizone to form lunula. They are crescentic in shape with a concavity towards the aperture. All collabral and longitudinal elements are weak in early ontogeny. Peristome ovate.

Discussion.—*Emarginula karuna* sp. nov. is similarly ovate and elevated as *Emarginula (Emarginula) conica* Lamarck (Knight *et al.*, 1960, figs. 140, 1a-c), the type species, which is a Recent form. But it differs mainly in ornamentation being characterised by axial ribs of variable strength. Moreover, selenizone is not depressed.

Emarginula (Tauschia) orthogonia Tausch, 1890 (Knight *et al.*, 1960, figs. 140, 11a-b), resembles the present form in



having similarly raised selenizone, but can be distinguished by stronger collabral ribs and absence of fine axial threads between the two stronger ones. Apex of the *E. (T. orthogonia)* is also more strongly curved.

Emarginula (Altmarginula) desnoyersi Eudes-Deslongchamps, 1842 (Knight *et al.*, 1960, figs. 140, 7a-b), is a Bathonian form that differs in shell size and ornamentation. The present species is larger in size, less elevated with raised selenizone and bears spiral elements, which the European form lacks.

The present species differs from *Emarginula (Emarginula) vadanaei* Toni, 1912 (Szabo, 1980, pl. 4, figs. 10-11; Conti and Monari, 1991, pl. 7, figs. 7-14), in shell size, ornamentation and curvature of the apex. The Bakony and Turkey specimens are smaller in size. Although they have similar slightly elevated selenizone, it extends for only about one-third of the shell height while in the present form it extends more than three-fourths of the shell height from the base. Furthermore, the present species is ornamented with strong longitudinal ribs and its apex is less curved.

Emarginula lepsuisi Gemmellaro, 1878 is another comparable Jurassic form. It can, however, be differentiated from the Kutch form by its convex shell along the selenizone and fewer ribs (see also Szabo, 1980).

Etymology.—The species is named in honour of late Karun Chandra Mitra, a renowned palaeontologist of the Department of Geological Sciences of Jadavpur University.

Suborder Trochina
Superfamily Trochacea
Family Turbinidae
Subfamily Angariinae

Genus *Helicacanthus* Dacquin Wenz, 1938

Type species.—*Turbo thurmanni* Pictet and Campiche, 1863; original designation.

Helicacanthus chanda sp. nov.

Figures 4-6, 7; 5-1, 2

Material.—Ten specimens, JUM/g 35-44. JUM/g 35 is designated holotype; the rest are paratypes. All specimens have their original shell preserved. Only two specimens are intact and the rest are lacking mostly their apical parts. All were collected from Bed 1, Jumara.

Diagnosis.—Average-sized *Helicacanthus* (about 18 mm high); height greater than diameter; a broad nearly flat ramp on upper surface, outer whorl concave; dense, fine prosoclineal striae on whorls and within umbilicus; both

carinae and cords may be granulated.

Description.—Shell of medium size, maximum height about 18 mm; thick, phaneromphalous turbiniform with height slightly greater than diameter. Apical angle ranges between 47° and 54°. Whorl at least 4 in number including protoconch and separated by strongly grooved suture. Protoconch dome-shaped, consisting of one and a half smooth whorls. Spire low, conical occupying about one-third of shell height. Body whorl large, rapidly increases in diameter, width slightly greater than height. A broad, nearly flat ramp on upper surface of whorls. Outer face of whorls narrow, slightly concave, bordered by two strong spiral carinae, first one being stronger. Prominent spiral cords 3 to 4 in number appear after second angulation and are restricted at base. Cords and occasionally carinae show regular granulation. Dense prosoclineal striae present on whorls and also within umbilicus. Aperture orbicular in outline, both outer and inner lips thick and base rounded.

Discussion.—The characteristic shell outline, presence of two strong carinae on outer whorls and apertural shape assure its generic position. The present species is distinguishable from the type species *Helicacanthus thurmanni* (Pictet and Campiche, 1863), (Knight *et al.*, 1960, fig. 204, 2) from the Aptian of Switzerland by its slender form and in ornamental features. The type species is ornamented with numerous spiral cords, which are present between the carinae and also within the umbilicus, whereas in the present species spiral cords are restricted only at the base and umbilicus is ornamented with dense axial threads.

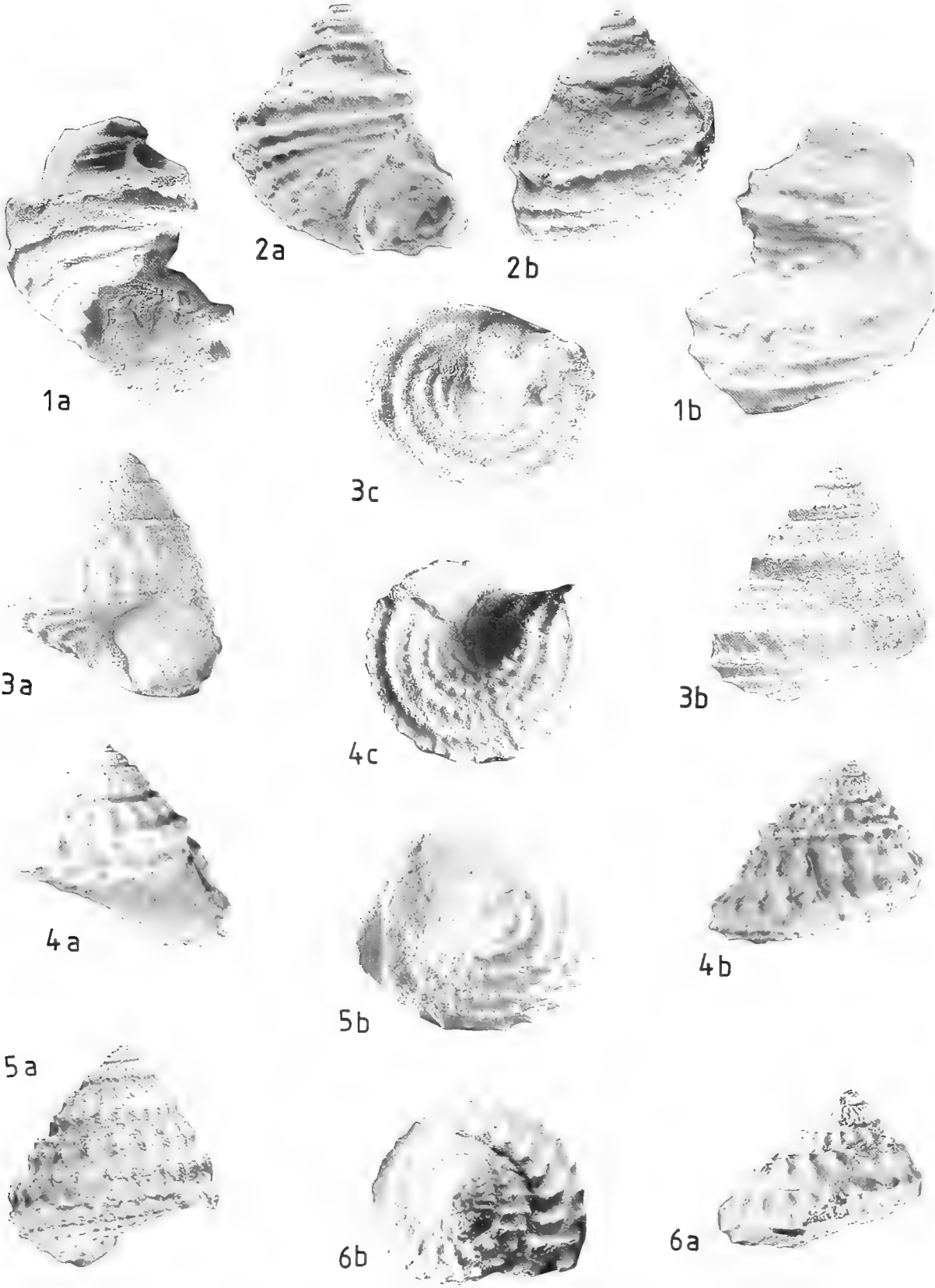
Cox and Arkell (1948-50) mentioned but did not describe one species of this genus, *Helicacanthus tegulatus* (Lycett) (1863, p. 102, pl. XLV, figs. 17, 18), from the Bathonian Forest Marble of England. Besides this, the present form is the second oldest species of the genus which otherwise ranges from the Upper Jurassic to Lower Cretaceous (see Knight *et al.*, 1960).

Etymology.—The species is named in honour of late S.K. Chanda, a famous sedimentologist of the Department of Geological Sciences, Jadavpur University

Family Trochidae
Subfamily Eucyclinae
Genus *Riselloidea* Cossmann, 1909

Type species.—*Risellopsis subdisjuncta* Cossmann, 1908; original designation.

← **Figure 4.** 1, 2. *Colpomphalus jumarensis* sp. nov. ×3. 1a-c. Holotype, from Bed 1, Jumara, JUM/g 19, apical, abapertural and basal views. Note strong collabral ridges and presence of three spiral carinae on body whorl (1b). 2a-c. Paratype, from Bed 2, Keera, JUM/g 595, apical, apertural and basal views. 3-5. *Emarginula karuna* sp. nov. Bed 1, Jumara, ×4. 3a-c. Holotype, JUM/g 71, protoconch missing; apical and two lateral views. 4. Paratype, apical part damaged, JUM/g 72, oblique lateral view showing selenizone (see arrow). 5. Paratype, both apical part and peristome damaged, JUM/g 73, oblique lateral view. 6, 7. *Helicacanthus chanda* sp. nov. from Bed 1, Jumara ×3. 6a, b. Holotype, complete shell, JUM/g 35, apertural and abapertural views. 7a, b. Paratype, complete shell, umbilicus showing axial ornamentation (7a), JUM/g 36, apertural and abapertural views.



Riselloidea tagorei sp. nov.

Figure 5-3-6

Material.—Over 300 specimens. JUM/g 148 is designated holotype; JUM/g 145-147 and JUM/g 149-166 are paratypes. Most of the specimens have their original shell preserved. All were collected from Bed 1, Jumara.

Diagnosis.—Medium to large-sized *Riselloidea* (10 to 15 mm high). Species shows wide intraspecific variation in shell profile with height greater than diameter changing to diameter greater than height; whorls cyrtocoid to straight; axial elements stronger than spiral ones; three spiral tuberculate carinae of variable strength and 3 to 4 basal cords with granulation.

Description.—Shell medium to large in size, maximum height being achieved 15 mm; weakly cyrtocoid to straight; trochiform and anomphalous. Apical angle ranges between 55° to 95°. Shell diameter may be greater or smaller than height. Whorls 4 to 5 in number including protoconch, which consists of two smooth, rounded whorls. Spire conical, low to moderately high, occupying one-fourth to one-third of shell height. Whorls regularly expanded, may be separated by relatively deep-channelled suture. Shell ornamented with three revolving carinae, third one is stronger than other two. First inter area forming a ramp, larger than that of second one which may sometimes be depressed. Relatively weak, prosocline riblets intersect carinae and produce pointed tubercles at crossing points. Axial elements running suture to suture, 20 in number on body whorl. Base weakly convex with 3 to 4 strong spiral cords with regular granulation resulting from interception of fine axial growth lines. Peristome is prosocline with thickened columellar lip. Aperture quadrangular to subquadrangular with angulations at middle carina and suture; outer lip thin.

Discussion.—Cossmann (1909) proposed the genus *Riselloidea* and designated his *Risellopsis subdisjuncta* Cossmann, as the type species. The present species resembles the type species in ornamentation and other general features but is relatively larger and has a rounded base.

The present species is very close to *Riselloidea biarmata* (Münster, 1844) (Cox and Arkell, 1948-50, p. 58; Knight *et al.*, 1960, fig. 203, 8) from the Great Oolite Series, England and the Middle Jurassic of Germany. However, it has a wide range of variation particularly in shell outline and larger shell size, quadrangular apertural outline, prosocline peristome and convex base. Moreover, it is ornamented with three tuberculate carinae whereas *R. biarmata* bears only two rows of tubercles.

Conti and Fischer (1982) described two new *Riselloidea* species from the Middle Jurassic sequence of Italy. These

species are very small in size and differ in some morphological aspects from the present species. *Riselloidea martariensis* Conti and Fischer (1982, pl. 3, figs. 11a-d, 12) differs, besides being small, in having a convex whorl outline and more depressed suture and in variation in number of axial elements.

Riselloidea subreticularis Conti and Fischer (1982, pl. 3, figs. 13a-d, 14), a smaller species than *R. martariensis*, resembles the present form in shell outline, but has a larger aperture, less dense axial ribs and convex whorl outline. In *R. subreticularis*, spiral cords appear only in the last whorl, while they are present right from the early whorls except for the protoconch, in the present species.

R. reticularis (Cossmann in Piette, 1864-91) (also see Conti and Fischer, 1982), a Bathonian species, has a close correspondence with the present species. It has comparable radial elements but differs mainly in having 4 spiral carinae instead of three and 5 to 7 basal cords instead of 3 to 4 in the present species. Further, we are not aware of any kind of intraspecific variation within *R. reticularis*.

Riselloidea multistriata (Böckh) (1874, p. 110, pl. VI, fig. 5) (also see Szabo, 1982, pl. 3, figs. 3-6) has a comparable size, but its convex whorls and dense, fine collabral cords distinguishes it from the Kutch form. Moreover, in *R. multistriata* basal cords are fine and more numerous, about 8 against 3 to 4 in the present population.

Etymology.—After the great Indian poet, R.N. Tagore.

Riselloidea elongata sp. nov.

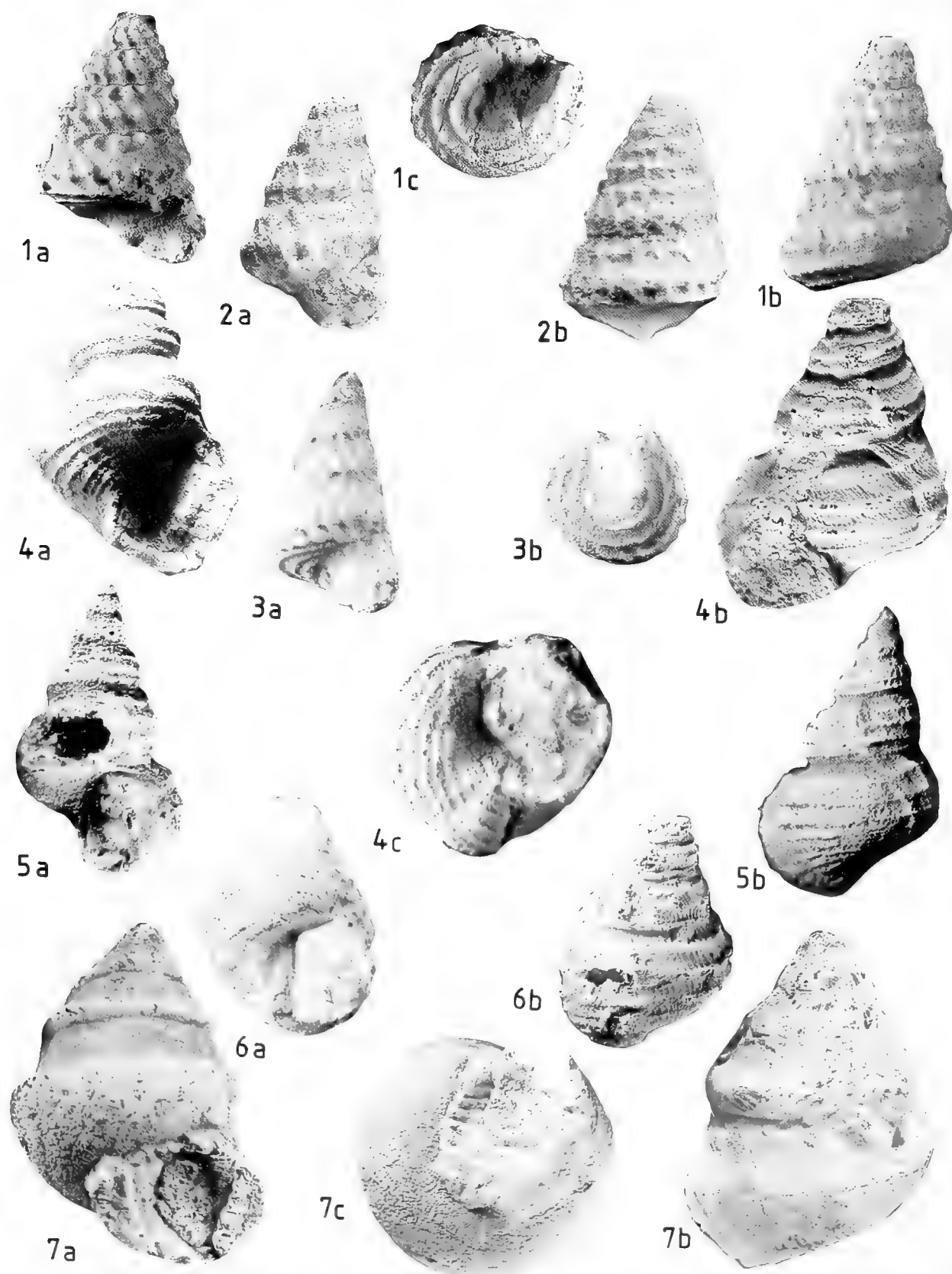
Figure 6-1-3

Material.—Seven specimens, JUM/g 138-144. Specimen JUM/g 138 is designated holotype; the rest are paratypes. The specimens have their original shell preserved. The present collection has been made from Bed 1, Jumara.

Diagnosis.—Large-sized *Riselloidea* (about 15 mm high); shell slender, height being twice shell diameter; whorls straight conical and numerous; base flat to weakly convex; two spiral, tuberculate carinae of equal strength, 3 to 4 basal cords with no granulation.

Description.—Shell slender, large, maximum height achieved 15 mm; anomphalous, trochiform; straight conical in outline, with height about twice the shell diameter. Apical angle ranges from 20° to 25°. Whorls numerous, seven in number including protoconch, which consists of two smooth and rounded whorls. Spire moderately long, occupying about half of shell height. Shell ornamented with two spiral carinae, more or less of equal strength, each bordering suture. Axial elements are weakly prosocline, running suture to suture. They are 20 in number on body whorl. Feeble tubercles are formed at intersecting points of trans-

← **Figure 5.** 1, 2. *Helicacanthus chanda* sp. nov. from Bed 1, Jamara, $\times 3$. 1a, b. Paratype, JUM/g 38, apertural and abapertural view; abapertural view (1b) showing dense axial striae. 2a, b. Paratype, almost complete, JUM/g 39, apertural and abapertural views. Note granulated basal cords in apertural view (2a). 3-6. *Riselloidea tagorei* sp. nov. from Bed 1, Jumara, $\times 3$. 3a-c. Holotype, complete shell, JUM/g 148, apertural, abapertural and basal views. 4a-c. Paratype, complete shell, JUM/g 157, apertural, abapertural and basal views. 5a, b. Paratype, complete shell, JUM/g 147, abapertural and basal views. 6a, b. Paratype, complete shell, JUM/g 159, abapertural and apical views.



verse and longitudinal elements. Base flat to weakly convex with 3 to 4 faint spiral cords. No granulation on cords at crossing points when intersected by very feeble axial growth lines. Aperture almost circular to subquadrangular; columellar lip thickened by callus; base narrow and slightly rounded.

Discussion.—*Riselloidea elongata* sp. nov. comes from the same stratigraphic level and geographic locality as *Riselloidea tagorei* sp. nov. These two species are comparable in having more or less similar size, conical and straight-walled shell outline, and nearly flattened base. *R. elongata* however, differs from *R. tagorei* in being more slender and high-spired. It has also more whorls and less shell rugosity, with only two rows of tubercles instead of three in *R. tagorei*. Besides, basal cords of *R. elongata* lack granulations, which are typical of *R. tagorei*.

The Kutch species has a close resemblance with *Riselloidea biarmata* (Münster, 1844), described from the Great Oolite Series, England and the Middle Jurassic, Germany (Cox and Arkell, 1948–50, p. 58, Knight *et al.*, 1960, fig. 203, 8). The present species, however, can be distinguished by its larger size, slender shape and absence of granulation on the basal cords.

The present species resembles *Riselloidea periniana* (d'Orbigny) (1853, p. 266, pl. 310, figs. 12, 13) (also see Fischer, 1997, p. 103, pl. 21, fig. 24) from the Plansbachian of France. Both species have a similar higher shell outline, high spire and surface ornamentation with two rows of tuberculate carinae. However, the older European form is smaller in height, having deeply grooved suture and more oblique axial riblets. Moreover, it has granulation at the basal cords, a feature which is absent in the present species.

Etymology.—After its elongated shape.

Genus *Onkospira* Zittel, 1873

Type species.—*Turbo ranellatus* Quenstedt, 1858; Original designation.

Onkospira kutchensis sp. nov.

Figure 6-4-6

Material.—Twenty-six specimens. JUM/g 45–70. JUM/g 45 is designated holotype; the rest are paratypes. All the specimens have their original shell preserved. Only two specimens are intact with the rest lacking their apical part. All were collected from Bed 1, Jumara.

Diagnosis.—Average-sized *Onkospira* (13 to 25 mm high);

whorls 5 in number including protoconch; spire short; strong spiral cords, 3 to 4 in number throughout ontogeny, basal cords 7 to 8; axial threads very fine, may be absent in some variants; two strong prosoclinal varices on each whorl, showing slight offset in successive whorls.

Description.—Shell medium in size, maximum height achieved about 25 mm; thick, anomalous and turbiniform with shell diameter about half of shell height. Apical angle ranges between 25° and 32°. Whorls 5 in number including protoconch. Protoconch consists of two smooth and rounded whorls. Spire highly elevated and about half of shell height. Whorls regularly expanding, strongly to slightly convex with sloping ramp. Suture impressed. Surface ornamented with 3 to 4 strong spiral cords throughout ontogeny and fine prosoclinal threads. Both are cancellate at their junction. Second and third cords from suture relatively stronger. Two strong prosoclinal varices located on each whorl and show slight offset on successive whorls. Last varix situated just behind outer lip. Basal cords are relatively fine and closely spaced, 7 to 8 in number. Aperture oval with its height slightly greater than width. Outer lip rounded and inner lip arcuate and reflected. Both lips are thick.

Discussion.—The turbiniform shell outline, convex whorl sides, predominance of spiral ornamentation and presence of varices are the characteristic features of *Onkospira*. From the above morphological description the generic position of the present species seems secure. So far, species of *Onkospira* have been reported from Europe and Japan ranging in age from the Upper Jurassic to Lower Cretaceous. The discovery of the present species brings down the lower limit of stratigraphic range of *Onkospira* as far as the Upper Bathonian.

The present form resembles *Onkospira gracilis* Zittel, 1873 (Knight *et al.*, 1960, fig. 203, 1) reported from the Tithonian of the Czech Republic. But *O. gracilis* is characterised by strongly convex, more numerous whorls, prominent collabral riblets and varices showing alignment on successive whorls.

The present species differs from *Onkospira haipensis* described by Kase (Kase, 1984, pl. 11, figs. 9–12) mainly in shell ornamentation. In some variants of *O. haipensis*, spiral cords are strong and tubercles are present at the intersection.

Etymology.—After Kutch, western India, from where the specimens have been collected.

? Subfamily Calliostomatinae

Genus *Proconulus* Cossmann, 1918

← **Figure 6.** 1–3. *Riselloidea elongata* sp. nov. from Bed 1, Jumara, $\times 3$. 1a–c. Holotype, JUM/g 138, apical part damaged; apertural, abapertural and basal views; note two rows of spiral carinae and basal cords lacking granulation. 2a, b. Paratype, apical part damaged, JUM/g 139; apertural and abapertural views. 3a, b. Paratype, complete shell, JUM/g 141, apertural and basal views. 4–6. *Onkospira kutchensis* sp. nov. from Bed 1, Jumara, $\times 3$. 4a–c. Holotype, apical part damaged, original shell preserved, JUM/g 45, apertural, abapertural and basal views; note slight offset of varices in last two whorls (4b). 5a, b. Paratype, complete shell, JUM/g 46, apertural and abapertural views. 6a, b. Paratype, apical part damaged, original shell preserved, JUM/g 47, apertural and abapertural views. 7a–c. *Proconulus jadavpuriensis* sp. nov. from Bed 1, Jumara, $\times 3$, Holotype, complete shell, JUM/g 76, apertural, abapertural and basal views; note abapertural view showing very fine opisthocline threads near aperture.

Type species.—*Trochus guillieri* Cossmann, 1885; original designation.

***Proconulus jadavpuriensis* sp. nov.**

Figures 6–7; 7–1, 2

Material.—Sixty-two specimens. JUM/g 76–137. Specimen JUM/g 76 is designated holotype; the rest are paratypes. Most of the specimens are intact and have the original shell preserved. JUM/g 81–86 were collected from Bed 7 and the rest are from Bed 1 of Jumara.

Diagnosis.—Average-sized *Proconulus* (15 to 20 mm high); smooth shell; whorls less numerous; flat in early stage, feebly concave later, periphery marked by angular keel; base feebly convex.

Description.—Shell small, maximum height 20 mm; anophalous, thick, conical; acute juvenile whorls; trochiform with height slightly greater than diameter. Apical angle ranges between 50° and 60°; whorls less numerous, five in number including protoconch, separated by impressed suture. Protoconch conical, consists of two smooth, rounded whorls. Spire moderately high, occupying about one-third of shell height. Whorls flat or feebly concave in early stage, concavity increases during ontogeny. Periphery is sharply angulate like a carina, which occurs just above suture. Body whorl large with diameter slightly greater than height. Shell smooth except for some fine prosocline threads, especially prominent near aperture of adult specimens; base rounded. Aperture circular to subquadragular, width of aperture slightly greater than height, base of aperture rounded. Both outer and inner lips thick, collumellar part has a thick callus.

Discussion.—The shell shape of the present species has a close correspondence with some species of *Epulotrochus* Cossmann, especially *E. epulus* (d'Orbigny, 1850). Szabo (1981), while describing the Hungarian Lower to Middle Jurassic gastropods, also observed the same similarities. Some smooth variants of his *Proconulus epuliformis* Szabo (1981, pl. 1, figs. 6–8) shows a striking resemblance to *E. epulus*. Szabo (1981) and Kase (pers. comm., 1992) acknowledged the need for a revision of these genera. The present species has thick callus and from the nature of the nucleus whorl and ornaments it is retained within *Proconulus*.

Present study includes numerous specimens, which enable us to examine both ontogenetic and intraspecific variations. The population shows low intraspecific variability.

The present species shows a resemblance in shell shape to *Proconulus rimosus* Szabo (1981, pl. 1, figs. 9–13), though the latter species has a wide range of variation in this respect. However, *P. rimosus* is an ornamental form with prominent spiral elements, which are even tuberculated in the early stage. The present species has a smooth shell except for some fine, faded axial threads which appear only at the adult stage in some variants. It is further characterised by slightly concave whorl and marked angular keel just above the suture.

Proconulus jadavpuriensis sp. nov. closely resembles

Proconulus brutus (d'Orbigny) (1853, p. 283, pl. ccxv, figs. 13–16) (Cossmann, 1885, p. 285, pl. vii, figs. 23, 24; Cox and Arkell, 1948–50, p. 59; also see Fischer, 1997, p. 112, pl. 19, figs. 6, 7) described from the Great Oolite of England. The latter species has a similar shell and apertural shape with a convex base, but differs in shell ornamentation, being characterised by five strongly tuberculate spiral bands and a very obscure suture while the present species has a smooth shell and very impressed suture. Besides, the present species has a concave whorl outline.

Proconulus epuliformis has a more or less similar whorl outline and smooth or feebly ornamented shell but differs in having a high conical shell, more numerous whorls and flattened base. Moreover, the present species is characterised by a well marked angular keel and impressed suture.

P. jadavpuriensis sp. nov. exhibits some degree of resemblance to the upper Bajocian species *Proconulus acanthus* (d'Orbigny) (1853, p. 273, pl. 312, figs. 9–12) (also see Fischer, 1997, p. 107, pl. 19, figs. 4a, b, 5) described from Port-en-Bessin (Calvados) in overall shell outline with angular periphery, size and apical angle. However, the present species differs from the latter in having a distinctly concave whorl outline, impressed suture and smooth shell except for some prosocline threads near the aperture, while the latter is distinguished by straight whorl outline and finely granular spiral cords.

Etymology.—After Jadavpur University.

Suborder Neritopsina
Superfamily Neritacea
Family Neritopsidae
Subfamily Neritopsinae
Genus ***Neritopsis*** Grateloup, 1832
Subgenus ***Neritopsis*** s. str.

Type species.—*Neritopsis moniliformis* Grateloup, 1832; original designation.

***Neritopsis (Neritopsis) patchamensis* sp. nov.**

Figure 7–3—5

Material.—Eight specimens. JUM/g 1–3, 5, 8–11. Holotype, JUM/g 1; the rest are paratypes. The specimens have their original shell preserved and were collected from Bed 1 of Jumara.

Diagnosis.—Small *Neritopsis* (8 to 11 mm high); whorls rounded with wide, gently sloping ramp; spire slightly protruding; whorls cancellated, both axial and spiral cords of equal strength, axial cords numerous (12 to 16) on body whorl; aperture very large, axially ovate with slight angulation near suture.

Description.—Shell small in size, maximum height about 11 mm, moderately thick, subglobose; height of shell about three-fourths of shell diameter. Apical angle ranges between 110° and 120°. Whorls rounded with wide gently sloping ramp, slightly angulate at suture. Protoconch not well discernible, but appears to be smooth and consisting of about two whorls. Spire short, body whorl very large and

increases rapidly in diameter. Suture impressed, running along a furrow. Whorls cancellated throughout later ontogeny, resulting from intersection of axial and spiral cords of equal strength. Axial cords 12 to 16 in number on body whorl, prosocline in beginning but becoming gentler during ontogeny. Spiral cords 10 to 14 in number on body whorl and irregularly spaced. Aperture very large, axially ovate and slightly angulate near suture; inner lip slightly thickened by callus accompanied by a shallow furrow running parallel to it and resulting in a pseudumbilicus.

Discussion.—*Neritopsis (Neritopsis) patchamensis* sp. nov. shows some degree of resemblance to the Lower and Middle Jurassic forms from Europe (Szabo, 1982; Conti and Szabo, 1989). It differs from *Neritopsis (Neritopsis) papodensis* Szabo (1982 pl. 1, figs. 6–9) in having a less protruded spire and less convex whorl surface with relatively broader ramp. It is coarsely ornate with stronger axial elements than in *N. (N.) papodensis*.

The present species, although it resembles strongly *Neritopsis abbas* Huddleston (1894, p. 341, pl. XXVII, figs. 11a–c) (also see Conti and Szabo, 1989, pl. 1, figs. 10–11) in shell shape, is much smaller in size with a less protruded spire. In *N. abbas*, spiral cords dominate with very faint axial growth lines near the aperture, but in the present species, axial elements are equally prominent and cut across the spiral cords resulting in a conspicuous cancellate ornamentation.

Neritopsis (Neritopsis) spinigera Szabo (1982, pl. 1, figs. 10–18) has been described on the basis of mostly damaged specimens. It, however, can be distinguished by its bicarinate ornamentation, long spine and fewer and stronger axial elements.

The Middle Jurassic (Bajocian–Bathonian) form *Neritopsis (Neritopsis) bajocensis* d'Orbigny (1852, p. 223, pl. 300, figs. 8–10; Fischer, 1997, p. 86, pl. 17, figs. 14a–c, 15a–c) can be compared with the present form in general globose shape and apertural outline. Close examination reveals that in the present species the height is less than the diameter while in the European form it is just the reverse. Further, the Kutch species has strongly cancellated ornamentation in the later ontogeny resulting from intersection of equally strong axial and spiral cords, but the European form has dominant spiral cords with very feeble axial elements. Besides, the Kutch species is less than half the size of *N. (N.) bajocensis*.

Etymology.—Refers to the Patcham Formation in which the species is exclusively confined.

Subgenus ***Hayamiella*** Kase, 1984

Type species.—*Neritopsis (Hayamiella) japonica* Kase, 1984; original designation.

Neritopsis (Hayamiella) sankhamala sp. nov.

Figure 7–6, 7

Material.—Ten specimens, JUM/g 4, 6, 7, 12–18. JUM/g 6 is designated holotype; the rest are paratypes. The specimens have their original shell preserved. The present collection has been made from Bed 1 of Jumara.

Diagnosis.—Small size for genus (6 to 8 mm high); narrow ramp, whorls bordered by subcarinate angulation; spire slightly protruding, suture impressed with a subsutural channel; cancellate ornamentation, axial element developed into varices, irregularly spaced, 6 to 9; spiral cords 9 to 13; prominent tubercles at intersection of spiral and axial elements; aperture circular to slightly axially ovate.

Description.—Shell small in size, maximum height achieved 8 mm; low-spired and naticiform. Shell diameter greater than height. Apical angle ranges between 105° and 122°. Narrow ramp, whorls bordered by subcarinate angulation. Protoconch seemingly smooth but number of whorls not discernible, may consist of more than one whorl, spire slightly protruding. Body whorl large, rapidly widening. Suture impressed with a prominent subsutural channel. Cancellate ornamentation with much stronger axial elements. Varices become stronger and interspace increases ontogenetically. Varices 6 to 9 in number on body whorl and orthocline. Spiral cords 9 to 13, strength varies, stronger ones irregularly intercalate with finer cords. Fine but prominent tubercles appear at intersection of spiral cords and varices. Aperture very large, near circular to slightly ovate axially; inner lip with narrow callus. Furrow running parallel to inner lip, resulting in a pseudumbilicus.

Discussion.—Kase (1984) erected a subgenus *Hayamiella* within the genus *Neritopsis* and described *N. (H.) japonica* Kase (p. 84, pl. 8, figs. 6a–c, 17) from the Upper Aptian of Japan as type species. He distinguished *Neritopsis* s. str. from *Hayamiella* on the basis of the presence of spiral cords, larger shell size and wider shell outline. He also admitted that distinction may not be very clear as there exist some intermediate forms (see also Hayami, 1960). The present species is characterised by small shell size, globose shape and coarsely cancellated ornamentation with much stronger axial elements, but it has a wider shell outline. Because of the similarities in many diagnostic characters we place the present species within the subgenus *Hayamiella*.

The present species has similarities with the type species *N. (H.) japonica* in many important morphological characters like small shell size, globose shape and cancellated ornamentation, so that their inclusion within the same subgenus is justified. However, *N. (H.) sankhamala* is still smaller in size, wider in outline and having fewer but stronger axial elements than *N. (H.) japonica*. Moreover, the type species comes from a higher stratigraphic horizon (Aptian).

The present species is closer to *Neritopsis (Neritopsis) patchamensis* sp. nov., but is relatively smaller in diameter with a narrower ramp area. Its axial elements are stronger and fewer on body whorl. Besides, it differs in having subcarinate angulation, tubercles, a circular aperture and a subsutural channel.

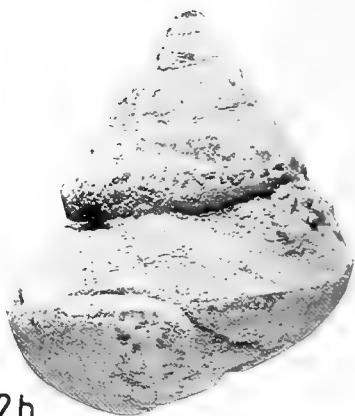
Neritopsis (Hayamiella) sankhamala sp. nov. is comparable to some European forms. It is close in size to *Neritopsis dumortieri* Conti and Szabo (1989, pl. 1, figs. 12–13) from the Southern Alps. This European species is based on the monotypic holotype, which is a damaged specimen. *N. dumortieri* bears three rows of spiral carinae and transverse elements of equal strength. Long hollow spines are present at the intersection point. The present species, on the other



2a



1b



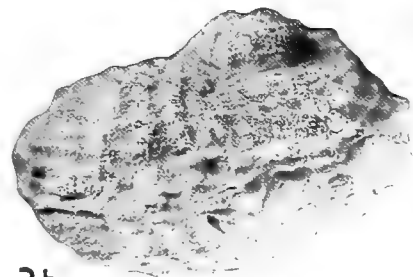
2b



3a



1a



3b



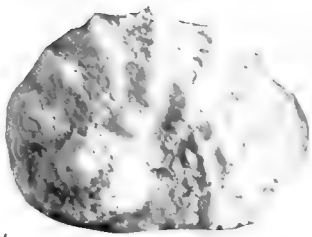
3c



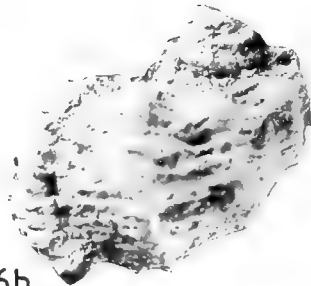
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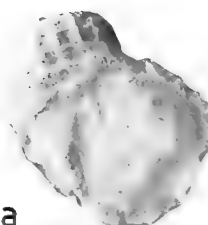
6a



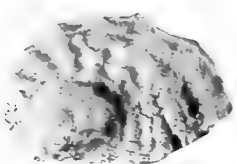
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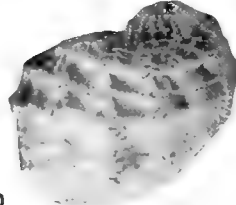
6b



7a



7c



7b

hand, possesses strong varices and small tubercles.

Neritopsis (Neritopsis) spinigera Szabo (1982, pl. 1, figs. 10–18) differs mainly in having a more closely ornate form with long spines and more protruded spire.

The present species shows a remarkable correspondence in size, shape and ornamentation to *Neritopsis (Neritopsis) elegantissima* Hörmes (1853, p. 763) (Szabo, 1982, pl. 1, figs. 1–3), but closer examination reveals that the Kutch form has a circular aperture, varices 6 to 9 in number, subcarinate angulation and tubercles. Moreover, *N. (N.) elegantissima* comes from a much older horizon of the Lower Jurassic (U. Sinemurian).

Neritopsis (Hayamiella) sankhamala sp. nov. has a close resemblance to *Neritopsis guerrei* Hébert and Deslongchamps (1860, p. 185, pl. I, figs. 4a–d) described from the Great Oolite of England (see also Cox and Arkell, 1948–50, p. 64). One variant even appears to be more close in having similar distant and unevenly placed axial elements. The present species, however, can be distinguished by its relatively distant spiral cords, stronger varices and presence of prominent tubercles.

Etymology.—Refers to an Indian ornament—a chain of small and globular gastropod shells

Genus *Hayamia* Kase, 1980

Type species.—*Hayamia rex* Kase, 1980 (in Kase and Maeda, 1980); original designation.

Hayamia mitra sp. nov.

Figure 8–1–3

Material.—Five specimens, JUM/g 31–34, 597. JUM/g 31 is designated holotype, the rest are paratypes. JUM/g 32, 33 are internal moulds, the holotype and one of the paratypes (JUM/g 597) represent composite state of preservation. JUM/g 34 with shell remains. JUM/g 31, 33 were collected from Bed 1, JUM/g 597, from Bed 6, JUM/g 32, from Bed 7 of Jumara; JUM/g 34 from Bed 2, Keera (see Bardhan *et al.*, 1994).

Diagnosis.—Medium-sized *Hayamia* (about 24 mm high); height less than diameter, spire slightly protruding, suture impressed with prominent subsutural channel, aperture large; prominent, numerous spiral cords with finer subordinate ones in between.

Description.—Shell medium-sized, maximum height achieved 24 mm; phaneromphalous; moderately thick, ovate and naticiform in outline with height of shell is about three-fourth of shell diameter. Apical angle ranges between 120° and 160°. Whorls rapidly expanding, convex in

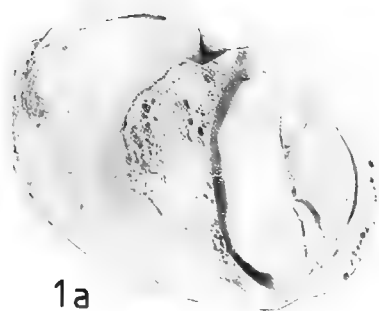
outline; whorls make two and a half volutions. Protoconch is not well discernible. Spire slightly protruding, about one-eighth of shell height. Body whorl very large, increases rapidly in diameter with a wide and weakly convex sutural ramp. Suture impressed with subsutural channel. Shell is ornamented with prominent and widely spaced spiral cords and several subordinate ones in interspaces; spiral elements are intercepted by very faint axial growth lines observed particularly near peristome; internal mould smooth. Aperture very large, elliptical in outline and expanded in direction oblique to axis. Height of aperture slightly greater than width. Both outer and inner lips thin and entire. Thin and somewhat obscure callus covers inner lip. Operculum thick, solid and elliptical in outline, its outer surface ornamented with both radial and concentric elements, abaxial part broken, but its adaxial margin has a curvaceous chevron shaped-outline.

Discussion.—Kase (1980) introduced the genus *Hayamia* (Kase and Maeda, 1980, pl. 35, figs. 3–10) in the family Neritopsidae from the Lower Cretaceous of central Japan to distinguish it from *Neritopsis*. The genus also includes some previously described Jurassic and Cretaceous species of *Neritopsis*. The main features which characterise *Hayamia* are spiral striae with or without costellae, absence of parietal tubercles and an elliptical operculum lacking any quadrangular process at the adaxial edge; although there is a certain amount of similarity with *Neritopsis*, these features probably confer an independent status to the genus. While *Hayamia* is included in the subfamily Neritopsinae, it has opercular feature resembling that of *Naticopsis* belonging to the subfamily Naticopsinae. Thus, it appears that *Hayamia* occupies an intermediate position between *Neritopsis* and *Naticopsis*. The actual phylogenetic relationship among the three genera is not yet clear (Kase, pers. comm., 1999) and has to be worked out by detailed study of properly weighted characters linking and separating them. In consonance with its genus the Kutch species *Hayamia mitra* sp. nov. has also a similar status and presently we place the species provisionally under the subfamily Neritopsinae.

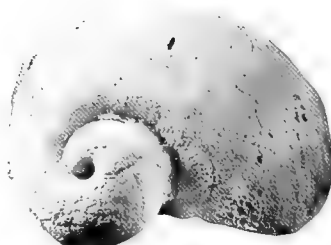
The Kutch species displays some resemblance to the type species *Hayamia rex* Kase (in Kase and Maeda, 1980, pl. 35, figs. 5–10) in size and surface ornamentation. But it differs from the latter in its overall shape with shell diameter measuring more than height, less protruded spire and slightly asymmetric elliptical operculum. *Hayamia chosiensis* Kase (in Kase and Maeda, 1980, pl. 35, figs. 3–4) also bears some similarity with the present species, but differs in having more dense spiral striae, more protruded spire and circular aperture with curved angulation at the adapical part.

Etymology.—The species is named in honour of late K.C. Mitra, a renowned palaeontologist in the Department of

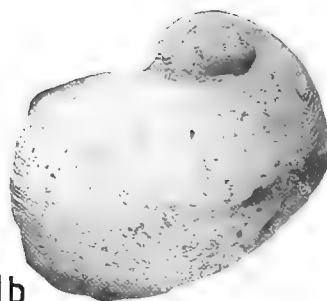
← **Figure 7.** 1, 2. *Proconulus jadavpuriensis* sp. nov. from Bed 1, Jumara, $\times 3$. 1a, b. Paratype, broken at apical part, JUM/g 77, apertural and basal views. 2a, b. Paratype, peristome slightly damaged, JUM/g 79, apertural and abapertural views. 3–5. *Neritopsis (Neritopsis) patchamensis* sp. nov. from Bed 1, Jumara, $\times 3$. 3a–c. Holotype, JUM/g 1, apertural, abapertural and apical views; apical view showing closely spaced axial cords. 4. Paratype, JUM/g 3, apical view. 5. Paratype, body whorl broken, JUM/g 9, abapertural view. 6, 7. *Neritopsis (Hayamiella) sankhamala* sp. nov. from Bed 1, Jumara, $\times 4$. 6a, b. Holotype, JUM/g 6, apical and abapertural views showing distant and strong axial cords. 7a–c. Paratype, young shell, JUM/g 16, apertural, abapertural and apical views.



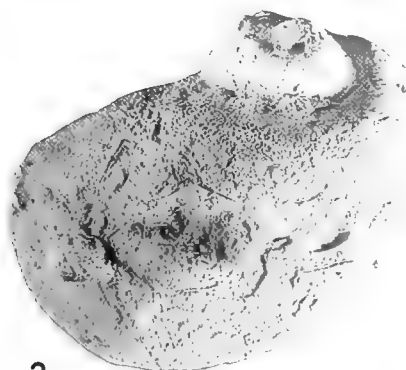
1a



1c



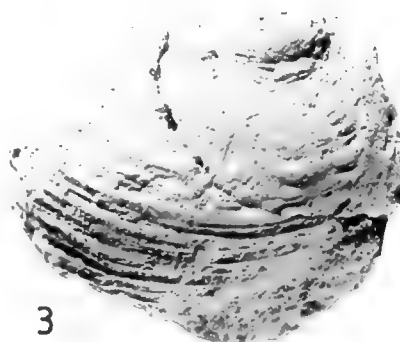
1b



2a



2b



3



4a



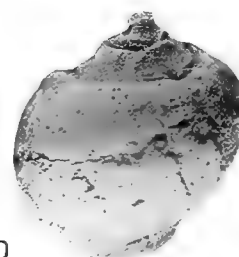
4b



6a



5



6b

Geological Sciences of Jadavpur University.

Order Caenogastropoda
Superfamily Naticacea
Family Naticidae
Subfamily Globulariinae
Genus *Globularia* Swainson, 1840

Type species.—*Ampullaria sigaretina* Lamarck, 1804; original designation.

Globularia spathi sp. nov.

Figure 8-4—6

Material.—Eight specimens. JUM/g 23-30. Holotype, JUM/g 23; the rest are paratypes. Three specimens are intact and rest are broken. Mostly internal moulds, in three specimens (JUM/g 23, 24, 25) part of the original shell is preserved. JUM/g 23 was collected from Bed 1, JUM/g 24, 26-30 from Bed 7 of Jumara and JUM/g 25 from Keera.

Diagnosis.—Medium-sized *Globularia* (about 30 mm high); spire relatively high; suture impressed throughout; umbilicus narrowly open, sheath narrow; aperture subelliptical; ornamented with fine prosoclineal growth lines conspicuous near aperture.

Description.—Shell of medium size, maximum height about 30 mm; globose, moderately thick, phaneromphalous and naticiform in outline with height slightly smaller than diameter. Apical angle ranges from 95° to 106°. Whorls at least five in number, separated by deeply channelled suture bordered by sharp periphery. Protoconch not discernible. Spire relatively high, obtusely conical, occupying about one-fourth to one-sixth of shell height. Body whorl with height slightly higher than diameter. Whorls convex, angulation present near suture. Whorl surface ornamented with fine prosoclineal growth lines conspicuous near aperture. Aperture wide, subelliptical in outline, with height nearly twice width, acute above and broadly rounded below. Parietal area covered by thick callus. Umbilicus narrowly opens; sheath narrow.

Discussion.—In a recent major taxonomic revision of the family Naticidae, Kabat (1991) has stabilised many family and genus level names. He removed *Natica fluctuata* G.B. Sowerby, 1825 from *Globularia* and designated it as the type species of *Cernina* Gray, 1847.

This is the largest naticiform species collected from Kutch. *Globularia* (*Nangkulania*) *puruensis* (Martin, 1914) (Wenz, 1941, fig. 2933) has a very short spire, both axial and spiral threads and a large aperture. In the present species, the spire is comparatively long, only prosoclineal growth lines are present

as surface ornamentation and the aperture is smaller than that of *G. (N.) puruensis*.

The present species can be compared with *Globularia* (*Globularia*) *izumiensis* Kase (1990, figs. 2.16-22, 2.25). Kase's species has a shell diameter greater than the height, low spire, and weakly impressed suture in early whorls. Further, it has a flattened upper whorl surface and subovate aperture. In contrast, the present species has a shell diameter smaller than its height, a more protruding spire, and a strongly impressed suture all through during growth. Aperture is subelliptical and whorls have a convex upper surface with angulation near the suture.

The present species resembles *Globularia rupellensis* (d'Orbigny) (1852, p. 203, pl. 293, figs. 1-3) (see Fischer, 1997, p. 77, pl. 16, figs. 1a, b, 2) from the Oxfordian—Kimmeridgian of Europe in general shell outline, apical angle, apertural shape etc. But the European form is much larger, the largest being about three times that of the present species. However, the obvious difference lies in the nature of the ornamentation. *G. rupellensis* is characterised by spiral striae with punctuation along their alignment, whereas the Indian species is ornamented with fine prosoclineal growth lines. Moreover, the suture of the present species remains deeply impressed all through ontogeny.

The present species is comparable with *Globularia zangis* (d'Orbigny) (1852, p. 198, pl. 291, figs. 10-11) (also see Fischer, 1997, p. 74, pl. 15, fig. 9) from the Callovian of France but differs in having a smaller shell size, higher apical angle and flatter outer whorl surface in early ontogeny. The ornamental aspects, however, cannot be compared since the holotype of the European form is an internal mould.

A close correspondence can be observed between the present species and *Globularia*? sp. described by Sohl (1965, pl. 4, figs. 10-15) from the Middle Jurassic Carmel Formation of Utah, North America. Sohl's specimens are undoubtedly *Globularia* with the diagnostic narrow sheath. Sohl compared them with some British Jurassic gastropods (Cox and Arkell, 1948-50, p. 83). His form is similarly high-spired like the present species, but is smaller and less globose. The smoothness of the American specimens, however, may be attributed to complete silicification, which might have destroyed the finer details of ornamentation.

Etymology.—Named in honour of L.F. Spath, a famous palaeontologist.

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— **Figure 8.** 1-3. *Hayamia mitra* sp. nov. $\times 2$. **1a-c.** Holotype, JUM/g 31, from Bed 1, Jumara, apertural, abapertural and apical views; mostly internal mould, part of shell remains near aperture, apical part damaged, well preserved operculum. **2a, b.** Paratype, internal mould, from Bed 1, Jumara, JUM/g 33, abapertural and apical views. **3.** Paratype, from Bed 2, Keera, JUM/g 34, with shell remains, showing spiral ornaments of variable strength, abapertural view. **4-6.** *Globularia spathi* sp. nov. $\times 2$. **4a, b.** Holotype, from Bed 1, Jumara, JUM/g 23, mostly shell remains, showing axial ornamentation; apertural and abapertural views. **5.** Paratype, from Bed 7, Jumara, JUM/g 24, abapertural view. **6a, b.** Paratype, young shell, internal mould, from Bed 7, Jumara, JUM/g 26, apertural and abapertural views.

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Hilgendorf's planorbid tree—the first introduction of Darwin's Theory of Transmutation into palaeontology

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Abstract. Franz Hilgendorf (1839–1904)'s palaeontological studies on the Miocene planorbid snails of the Steinheim basin (Germany) frame his scientific work from his dissertation in 1863 to his last publication on this subject in 1901. Hilgendorf discovered that the different planorbids are not mixed in each layer, and noticed gradual transitions between different morphs of successive layers. These findings led to his hypothesis of species transmutation illustrated by his planorbid tree. This was the first phylogenetic tree reconstructed on the basis of real fossil evidence, and therewith it was the first palaeontological example of Darwin's Theory of Transmutation. Although Hilgendorf did not refer to Darwin emphatically, he can be called the first one who introduced Darwin's Theory of Transmutation into palaeontology.

Key words: Hilgendorf, phylogenetic tree, planorbids, Steinheim, theory of transmutation

Introduction

Franz Hilgendorf is famous mainly for his zoological work, of which the Hilgendorf Exhibition (Yajima, 1997, 1998) focused on his merits for ichthyology and fishery sciences in Japan. However, his palaeontological work is no less important. Hilgendorf started his scientific career with a palaeontological study on the Miocene planorbid snails of the Steinheim basin. This was the subject of his dissertation (Hilgendorf, 1863) and of his first publication (Hilgendorf, 1866), and although he was later on mainly concerned with zoological subjects, the Steinheim snails remained on his mind for the rest of his life. His last paper on the Steinheim snails was published three years before his death (Hilgendorf, 1901). Thus, the planorbid studies frame his scientific work.

Already in his first study Hilgendorf recognised gradual transitions between the snails of successive layers. He documented and interpreted these findings in his first publication with a phylogenetic tree, which is the first palaeontological documentation of species transmutation. His hypothesis, heavily disputed at that time, was largely confirmed over the last two decades (Mensink, 1984; Gorthner, 1992; Povel, 1993; Nützel and Bandel, 1993; Finger, 1998).

Although Hilgendorf's findings were most important for the discussion of Darwin's Theory, which was published only few years before (Darwin, 1859), Hilgendorf did not refer emphatically to Darwin in his papers. On the other hand, Darwin himself mentioned Hilgendorf in his sixth edition of the 'On the origin of species.', published in 1872, within Chapter 10 (On the imperfection of the geological record), subchapter 'On the absence of numerous intermediate varieties in any

single formation', as follows: "... Hilgendorf has described a most curious case of ten graduated forms of *Planorbis multiformis* in the successive beds of a fresh-water formation in Switzerland" [wrong geographic information by Darwin]. Hilgendorf's historical role has been already recognised by Abel (1929), and the significance of Hilgendorf's studies from a Neo-Darwinian point of view is discussed in detail by Reif (1983a, 1983b, 1985, 1986).

To assess whether Hilgendorf was familiar with Darwin's Theory, the present paper gives a brief chronological survey of Hilgendorf's planorbid studies, paying special attention to remarks on Darwin and Darwinism. Finally, a brief account of the research on the Steinheim snails after Hilgendorf's death with emphasis on the connection between Hilgendorf's contribution and the latest work at Steinheim is added. Before that, some information about the Steinheim basin, and also the state of knowledge of the Steinheim snails before Hilgendorf are given.

The Steinheim basin—a meteorite crater

The Steinheim basin is situated on the Swabian Alb in southern Germany (Figure 1). Today it is known that the basin was formed by a meteorite impact, about 15 million years ago, which is, expressed in geological time, the Middle Miocene of the Tertiary. The Steinheim basin is a complex impact crater structure with an almost circular outline, and a central uplift, called the central hill. The basin has a diameter of about 3.5 km, and is 120 m deep today. Soon after the impact the crater filled with water and became a lake. It is supposed that the water supply came mainly from the subterranean karst system and from precipitation. How



Figure 1. Location of the Steinheim basin.

long the lake actually existed is not exactly known. Between some hundreds of thousands to two million years are suggested. This is what we today call a long-lived lake (Gorthner, 1994). At the end of the lake period the basin was completely filled with lake sediments. The fact that we can recognise the basin again today is due to partial erosion during the Quaternary, the last two million years. However, the lake sediments preserved reach a thickness of 30 to 40 meters, and are very rich in well preserved fossils. About 100 species of fossil plants and more than 250 species of fossil animals have been found so far. The snails comprise about 100 species, of which the planorbids are the most abundant group.

The knowledge of the Steinheim snails before Hilgendorf

In 1862 when Hilgendorf started his studies not much was known about the Steinheim basin, neither about its origin nor its palaeontology. However, the occurrence of amazing quantities of calcareous shells within the Steinheim sands was documented for the first time already about 150 years before, by the physician Lentilius (1711). Lentilius was fascinated by the amount and multiformity of these shells, and it seemed to him enigmatic for what reason God had created such a variety of tiny shells (Figure 2). At that time it was not yet known that these shells are remains of once living animals, what we call today fossils, but it was believed that all species were created by God and remained unchanged since their creation. This dogma of the fixity of species was still universal when the study of von Klein (1847) was publi-



Figure 2. Ensemble of Steinheim snails within the sediment (photo : H. Lumpe, Staatliches Museum für Naturkunde Stuttgart). The width of the shells is about 4 to 5 mm.

shed. Von Klein's study is one of the first scientific studies of the Steinheim snails and reflects the latest knowledge about this subject at the time when Hilgendorf started with his studies. Von Klein distinguished five planorbid species, four of which he allocated to the genus *Planorbis*, and one to the genus *Valvata*. From the latter species, called *Valvata multiformis*, he distinguished five varieties. According to von Klein all of these species and varieties occurred always mixed within each layer of the Steinheim deposits.

Hilgendorf's dissertation and first publication

Before Hilgendorf went to Tübingen he had studied in Berlin for two years. He came to Tübingen in 1862, attracted by Friedrich August Quenstedt, in order to study palaeontology. Quenstedt was a professor of geology and palaeontology at the University of Tübingen, and became famous by his comprehensive stratigraphical investigations of the Jurassic Swabian Alb by means of ammonites. In the autumn of 1862, Hilgendorf accompanied Quenstedt on an excursion to Steinheim, during which he first became acquainted with the Steinheim basin and its snails.

By collecting snails in Pharon's sand pit on this excursion, as well as during the following weeks, Hilgendorf discovered that the different varieties of *Valvata multiformis* are never mixed, but that they occur separately in the different layers. From the lowermost beds onwards he noticed a sequence of flat or planispiral shells to trochispiral shells and again to planispiral ones in the upper parts of the section. Moreover, the different morphs were connected by transitional morphs. Most surprising was the discovery that transitions were not only found between the different varieties of *Valvata multiformis* but also between species of *Planorbis* and some of the varieties of *Valvata* – in other words: he found gradual transitions between two different genera. These findings, of course, were not compatible with the dogma of the fixity of species.

Hilgendorf stated these findings in his dissertation which was submitted in spring, 1863. His dissertation comprises 42 pages, and does not include any figures. In the 1980s Prof. Wolf-Ernst Reif from the Palaeontological Institute of the University of Tübingen discovered a collection of 25 cards of thick paper with Steinheim snails glued onto it which could be clearly identified as Hilgendorf's, because of hand-written captions on the cards (Reif, 1983a).

While each of the cards from no. 1 to no. 17 contains snails of different beds, the cards no. 18 to no. 25 illustrate transitions from one taxon to another, and card no. 24 gives a complete phylogenetic diagram of Hilgendorf's results. Reif (1983a) reconstructed a phylogenetic diagram according to card no. 24 (Figure 3). It corresponds fairly well with Hilgendorf's interpretation given in his dissertation, and shows three modes of species transformation in course of time: 1. gradual transformation, 2. splitting into two daughter species, and 3. fusion of two species.

Actually, Hilgendorf never seriously suggested fusion of lineages, but merely raised it as a doubtful possibility. Considering the planorbid varieties of the third layer (see Figure 3, layer D), he raises the question of whether fusion of

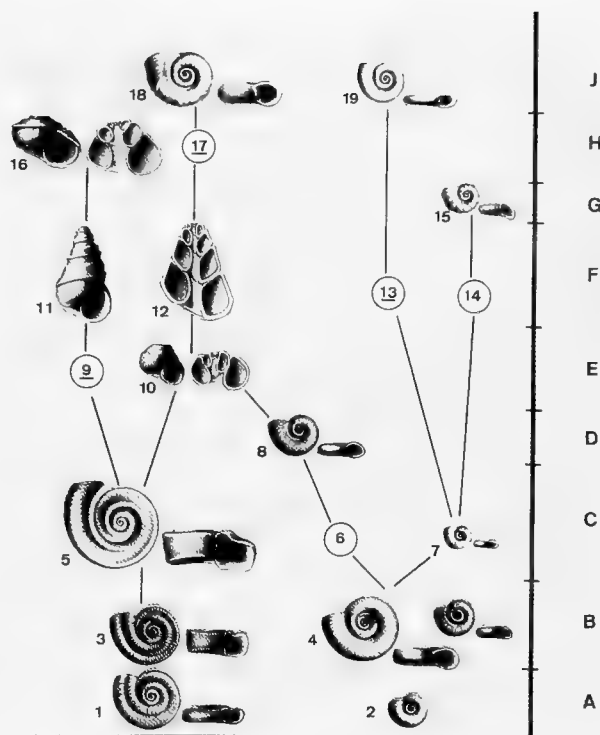


Figure 3. Reconstructed phylogenetic diagram of Hilgendorf's dissertation according to card no. 24. Circled numbers: either not identifiable (underlined) or missing. Examples for species transformation are: 1. gradual transformation: sequence from no. 1 to no. 5; 2. splitting into two daughter species: no. 5 splits into no. 9 and no. 10; 3. fusion of two species: no. 8 and no. 10. Reproduced from Reif (1983a, fig. 3) with permission of Paläontologische Gesellschaft.

two varieties could have led to this situation (Hilgendorf, 1863, p. 26). However, on the last page of his dissertation, there is an additional note to this subject (Hilgendorf, 1863, p. 42): "Darauf würde das schöne Bild, das Darwin uns vom Zusammenhange der Spezies in einem Zweige-reichen Baume vorführt, nicht passen, die Zweige eines Baumes wachsen nicht wieder zusammen." [This does not fit the nice picture of a tree with many branches which Darwin presented to illustrate the descent of the species – the branches of a tree never fuse again]. This note also exemplifies that Hilgendorf was already acquainted with Darwin's Theory during his first study.

Already after one year at Tübingen Hilgendorf went back to Berlin and continued his studies of natural sciences, especially organic chemistry, but subsequently he concentrated more and more on zoology. He got a position at the Humboldt Museum, and in 1865 he again started an investigation of the Steinheim snails, which was supported by the Royal Prussian Academy of Sciences. This new field work at Steinheim took two months and led to his first publication (Hilgendorf, 1866), which is still today the crucial publication on the Steinheim snails.

This paper is based on a study of a large amount of

material collected thoroughly bed by bed from three sand pits around the central hill, as well as from the western margin of the basin. Already the title of this paper: "*Planorbis multiformis* im Steinheimer Süßwasserkalk" [*Planorbis multiformis* within the calcareous freshwater deposits of Steinheim], reveals Hilgendorf's solution of the taxonomic problems, which confronted him through his findings. He considered all planorbid snails found to belong to one species, *P. multiformis*. And the subtitle: "Ein Beispiel von Gestaltveränderung im Laufe der Zeit" [An example of morphological change during time], so to say, gives an explanation for his solution. Moreover, this is also a clear confession of belief in Darwin's Theory of Transmutation.

However, Hilgendorf did not refer to Darwin in this paper. The first part of the publication comprises a detailed stratigraphical description of the sections, and a morphological characterisation of the 19 varieties or subspecies of *P. multiformis* which he distinguished. Using the biostratigraphical distribution of these subspecies, Hilgendorf subdivided the Steinheim deposits into ten zones or beds. In the second part of the paper he discussed the transitions between subspecies of successive beds. By arranging the subspecies in a stratigraphical scheme and marking transitions between two subspecies by a connecting line, Hilgendorf's phylogenetic tree became graphical. The planorbid tree is illustrated in the middle of the lithographic plate at the end of the paper, surrounded with illustrations of all subspecies, including also cross-sections of the snails.

Figure 4 shows a reconstructed and magnified version of this tree. The whole tree arises from a small and planispiral planorbid, called *aequeumbilicatus*, which is considered the founder population. The branch at the right hand comprises ten bigger morphs. Today, this branch is called the 'main branch', and is the most studied and discussed part of the tree so far. Especially the transition between the trochispiral form *trochiformis* and the planispiral form *oxystomus* later became a subject of controversial discussions. While the second branch, in the middle of the tree, splits from the *steinheimensis* form, and comprises only two forms, the third branch, at the left hand, splits from the founder population, and comprises seven forms. Today, these two branches are called the 'side branches'.

In contrast to the diagram reconstructed by Reif (1983a), according to Hilgendorf's cards and dissertation, this new tree involves only two modes of speciation: gradual transformation and splitting, but no fusion. Additionally, the whole tree arises from one founder species. This interpretation was compatible with Darwin's Theory.

The controversy with Sandberger

There was no critical reaction to Hilgendorf's publication for the first few years, but during the time Hilgendorf was in Japan, Fridolin von Sandberger started to controvert Hilgendorf. Sandberger was a professor of geology at Würzburg, and he was reputed to be an authority on fossil snails. By three very short articles (Sandberger, 1873, 1874a, 1874b), he totally rejected Hilgendorf's interpretation. Sandberger neither accepted the allocation of all Steinheim planorbids to

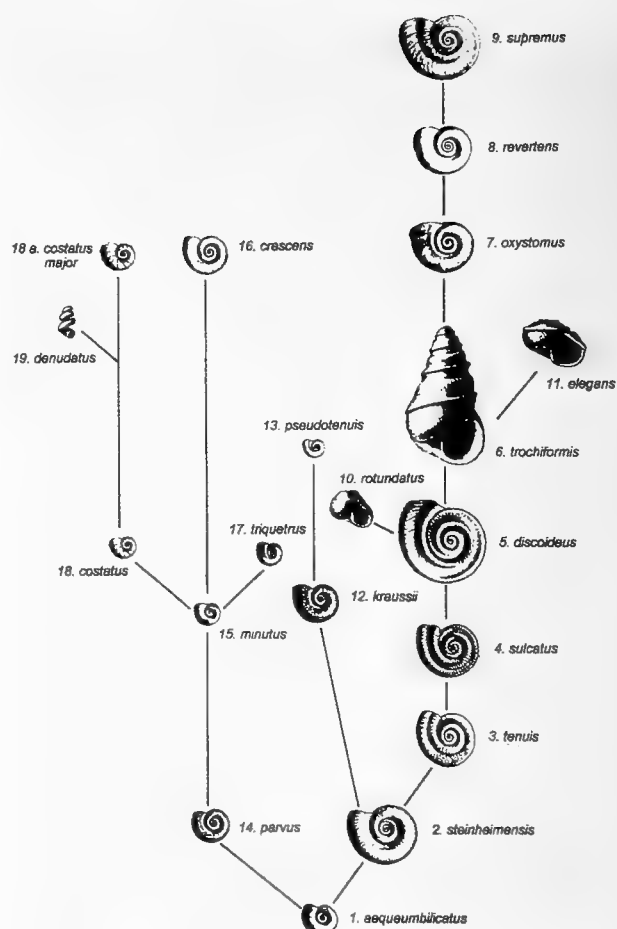


Figure 4. Reconstructed version of Hilgendorf's 1866 planorbid tree.

one species, nor the occurrence of the different varieties of *Valvata* in a stratigraphically orderly fashion, nor the transitions, but sustained von Klein's concept, and thus the fixity of species.

Hilgendorf got wind of Sandberger's criticism in Tokyo, and commented on it in November 1874, with a letter to his friend Eduard von Martens, which was published in the "Zeitschrift der Deutschen Geologischen Gesellschaft" (Hilgendorf, 1875). The controversy lasted till 1877 and reached its summit at the 'Meeting of Natural Scientists and Physicians' in Munich. Although the dispute exemplifies Hilgendorf's excellent attitude of being always obliged to the facts, I do not want to discuss it in detail (see Hilgendorf 1877a, 1877b, 1877c, 1877d). Summarising, the following assessment can be given:

1. The background of Sandberger's attacks had been only to a minor extent a dispute against the validity of Darwin's Theory. Unfortunately, the dominant motivation for his rigid attitude apparently was his antipathy toward the Prussians (see Hilgendorf, 1879, p. 90).

2. However, responding to Sandberger's accusation, Hilgendorf had checked his findings again and again by field

investigations, and had found more evidence of his hypothesis.

3. Despite the trouble that Hilgendorf had to suffer from this controversy, another positive effect was that his findings became well known in professional circles, and finally most of the experts accepted his hypothesis.

In order to demonstrate the stratification, as well as the transitions, at the Munich Meeting, Hilgendorf had collected new material and had taken photographs during his third season of field activities in Steinheim, which took nine weeks. One of these photos, actually assembled from two photos, is a panoramic view of the western side of the central hill. At that time, the sand pit had still a large expanse. Another photo taken by Hilgendorf himself shows a detail of Pharion's sand pit, obviously taken to demonstrate the stratification, because it shows the same part of Pharion's sand pit as a sketch drawn by Hilgendorf.

Hilgendorf's planorbid papers after 1877

Concerning Hilgendorf's familiarity with Darwin's Theory, his publication of 1879 (Hilgendorf, 1879) provides most clear evidence. This paper was published in the journal "Kosmos" which was founded only two years before, in 1877, for the purpose of promoting the concept of natural evolution. On the editorial board appear the names of Charles Darwin and Ernst Haeckel. Haeckel was the most prominent exponent of Darwinism in Germany, and had coined the term "Phylogenie" in 1866.

Hilgendorf (1879) gives a full account of his data and his theoretical concepts. The paper contains a newly drawn phylogenetic tree, showing most of the snails in cross-sections (Figure 5). The tree is almost identical with that of 1866, except that the founder population is missing. Already in 1866 Hilgendorf was in doubt whether there was only one planorbid form in the lowermost beds from which all the other forms had been developed. Now he withdrew this hypothesis, because it seemed to him that too little was known about the deposits on the western margin of the basin where this form occurs. In this paper Hilgendorf also formulated a concept for the recognition of evolutionary lineages in palaeontology including the practical method of bed-by-bed investigation. Finally, he summarised his data and his interpretations in 27 theorems. These theorems also contain problems and hypotheses, which became a subject of discussion only later, for example the law of irreversibility of evolutionary changes. Nevertheless, Hilgendorf did not speculate on the reasons for the species transmutation in the Steinheim basin. This seemed to him still too early, but he gave some hints for further investigations, for example to check the embryonic part of the gastropod shells, which should provide evidence for speciation, and to check other groups of Steinheim fossils for transmutation (Hilgendorf, 1879, p. 94 and 98). Hilgendorf mentioned in his paper of 1879 also the findings of Neumayr and Paul (1875) who had also found gradual transformations in Tertiary gastropods of Slovenia. In a footnote of their paper they credited Hilgendorf as the first one who had provided evidence for gradual transformation by a detailed palaeontological study.

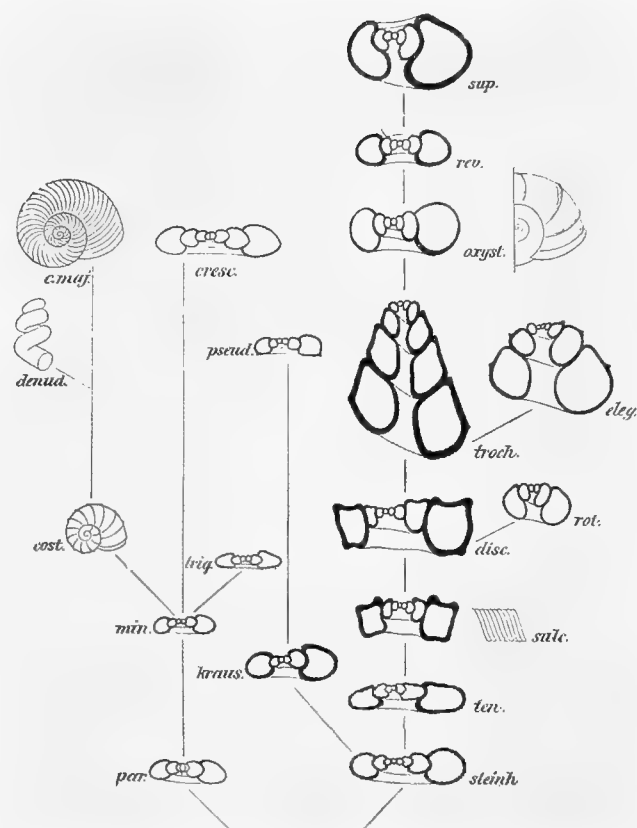


Figure 5. Planorbid tree of Hilgendorf (1879). Reproduced with permission of *Kosmos*.

After 1879, two additional papers of Hilgendorf (1881, 1901) on the Steinheim snails were published. In 1881 he commented on the paper of Hyatt (1880). Hyatt was an American scientist, who had been studying the Steinheim snails since 1872. Then, Sandberger had claimed that Hyatt's view would support his statements and would disprove Hilgendorf's interpretation. But in fact, Hyatt was a Darwinian, and was attracted to this study by Hilgendorf's first publication. Generally speaking, Hyatt's findings support Hilgendorf's interpretation, except for some differences in the question of the stem species and the transition between the trochospiral and the planispiral form. Moreover, Hyatt promoted Hilgendorf's subspecies to species rank.

In his last paper Hilgendorf (1901) once again took care of the most disputed transition between the trochospiral and the planispiral form, and illustrated the transitions by a series of photographs.

The planorbid tree after Hilgendorf's death

From 1901 to the present day more than 30 papers on the Steinheim planorbids have been published. Till the beginning of the last decade the most important steps confirming Hilgendorf's findings were made by Gottschick (1920) and Wenz (1922), as well as Mensink (1984). Gottschick and Wenz have been the first who examined again the Steinheim

snails of all beds in detail. Although, in contrast to Hilgendorf, they regarded the morphological changes of the planorbids as ecophenotypic, they fully confirmed the occurrence of the different morphs within the different beds. Mensink also studied the planorbids of all beds, and additionally he checked the occurrence of Hilgendorf's main branch planorbids at a large number of sites spread over the whole Steinheim basin. Moreover, Mensink demonstrated the gradual transitions of the main branch planorbids by means of biometrical investigations. The significance of Gottschick's and Mensink's results are discussed in detail by Reif (1985), and recently, Mensink's data set was reconsidered by means of multivariate methods (Povel, 1993).

In connection with Hilgendorf's (1879) hints for further investigations mentioned above, *i.e.*, to study the embryonic part of the shells and to check other groups of Steinheim fossils, both approaches were carried out only during the last decade, more than 100 years after Hilgendorf's publication. With respect to the embryonic part of the gastropod shells (protoconch), Gorthner (1992) and Nützel and Bandel (1993) were able to show by means of SEM analyses of the protoconch structures that both Hilgendorf's main branch and side branch planorbids are valid species. Moreover, the most recent study shows by such protoconch analyses that Hilgendorf's *aequeumbilicatus*, which is called *Gyraulus kleini* today, did not consist of three different species giving rise to three lineages as Gottschick (1920) suggested, but that *Gyraulus kleini* was the only founder species of the whole planorbid lineage (Finger, 1998).

Hilgendorf's second hint, to check other Steinheim fossils for morphological changes, was taken up in a detailed bed-by-bed study of the Steinheim ostracods (Janz, 1992, 1997). Ostracod shells are the most abundant fossils among the Steinheim deposits, and there are also some species which show morphological changes through the profile. In the genus *Leucocythere*, speciation by a splitting event was detected (Janz, 1992), and the splitting hypothesis could be supported by a detailed study of the microfeatures of *Leucocythere* shells by Viehofen (1997). Moreover, the ostracod assemblage shows a pattern of shell alteration through the profile similar to that of the planorbids (Janz, 1993, Janz, in press). As to the reasons for these alterations, on which Hilgendorf did not speculate, there are two major factors possibly provoking evolutionary changes in both snails and ostracods: long term ecological changes, as well as the longevity of the lake. While the long-term ecological changes were mainly due to lake level fluctuations, the longevity of the former Lake Steinheim was postulated by Gorthner and Meier-Brook (1985) because of the similarity of the heavily sculptured planorbids with endemic species of extant ancient lakes.

Conclusions

Summing up this brief chronological survey of Hilgendorf's studies on the Steinheim snails, it can be concluded:

1. By looking at Hilgendorf's palaeontological work more closely, it becomes evident that Hilgendorf was already a convinced Darwinian from the beginning of his studies.

2. Hilgendorf set a high value on demonstrating the objectivity of his methods of working based on an inductive approach, and perhaps for this reason did not refer to Darwin in his papers.

3. Nevertheless, he applied Darwin's Theory of Transmutation by his interpretation of the Steinheim snails, and therefore he can be called the first one to introduce Darwin's Theory into palaeontology.

4. Hilgendorf's interpretation has been generally confirmed by further studies, and hints he had given have led to findings supporting his hypothesis. However, there are still many questions to be answered, in order to fully understand the Steinheim planorbid tree.

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***Keraocarpon* gen. nov., magnolialean fruits from the Upper Cretaceous of Hokkaido, Japan**

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Abstract. Two new permineralized magnolialean fruits derived from the Coniacian–Santonian strata of the Upper Yezo Group are described in this paper. Each fruit consists of floral head, convex receptacle and woody peduncle. Floral head consists of many conduplicate follicles with adaxial opening. Follicle is long stalked, unilocular and many seeded. Since the fruits differ from the already known ones of Magnoliales, a new genus *Keraocarpon* is proposed to include two new species, *K. yasujii* and *K. masatoshii*. A brief comparison of *Keraocarpon* to other magnolialean taxa is made. These two new species are distinguished from each other by the differences in size of various elements, number of follicles in the aggregate fruits, number of seeds per follicle, and other minor characters. The genus is characterized by aggregate fruits of many seeded apocarpous stalked follicles on a slightly convex receptacle.

Key words: Aggregate fruits, follicle, Hokkaido, Japan, *Keraocarpon*, Magnoliales, Upper Cretaceous

Introduction

In 1980, Yasuji Kera collected a permineralized specimen of a magnolialean fruit from an ammonite-bearing floated nodule in the Kumaoizawa (brief map, see Ohana and Kimura, 1993, fig. 1), Mikasa City, Hokkaido. Around this locality, the fossiliferous Yezo Group of marine origin is exposed, and the coexisting ammonites indicate a Coniacian–Santonian age (Ohana and Kimura, 1991).

This specimen was briefly described by Ohana and Kimura (1987) as an unnamed magnolialean flower. Masatoshi Kera collected later a smaller specimen of the same kind along the bank in the upper course of the Ikushunbetsu River, which might be derived from the Upper Yezo Group.

After an extensive study of these specimens, this paper now describes them in detail as new fruits under a new name *Keraocarpon* gen. nov. Ohana, Kimura and Chitaley, with description of two new species *K. yasujii* and *K. masatoshii*. The genus and species described here have seeds inside the follicles and thus a new generic name *Keraocarpon* is better suited, instead of *Keranthus*.

Materials and methods

Both the fruits are permineralized. Their cells and minor structures are partly disintegrated by the subsequent crystallization of calcite. Two permineralized specimens are cut as indicated by arrows in Figure 2-2 and Figure 5-2.

Cutting surfaces were polished with carborundum abrasive and then etched with diluted HCl for half a minute. Peels on

cellulose acetate film were taken from the etched surfaces after washing off the acid with water. Cellulose-acetate film 0.034 mm thick ('Bioden, R. F. A.', Oken Co., Tokyo) was used to make the peel sections.

The specimens and their peel sections are kept at the Institute of Natural History, Tokyo (INH).

Systematic description

Class Magnoliopsida

Order Magnoliales (Family unknown)

Keraocarpon Ohana, Kimura and Chitaley gen. nov.

Etymology.—After Y. Kera who collected the type specimen of *Keraocarpon yasujii*.

Type species.—*Keraocarpon yasujii* Ohana, Kimura and Chitaley sp. nov.

Generic diagnosis.—*Keraocarpon* is a member of the woody polycarpous aggregated group of magnolialean fruit. Follicles stalked, many-seeded and spirally arranged on the receptacle.

Keraocarpon is unique in external form but vegetative parts and male organs are unknown. In transverse section, stalks have a large central pith, collateral bundles, and thin inner and thick outer cortices. The bundles consist of vascular elements with scalariform thickenings. Seeds: The follicle unilocular with many seeds alternately arranged in two rows. Seed coat thick with micropyle facing the adaxial suture of the follicle.

Remarks.—The new magnolialean genus *Keraocarpon* is

distinguishable from other magnolialean fossil genera with apocarpous and conduplicate follicles (e. g. *Archaeanthus*; Dilcher and Crane, 1984) in having a long receptacle. *Lesqueria* (Crane and Dilcher, 1984) has an ovoid receptacle and bifid distal end of the follicle. *Protomonimia* has a concave receptacle and sessile follicles (Nishida and Nishida, 1988).

Recently, a magnolialean fructification was reported by Nishida *et al.* (1996) from the Upper Cretaceous of Hokkaido. According to them, it has more than 170 short-stalked apocarpous and adaxially sutured follicles on the slightly concave receptacle. Follicle has a single dorsal and a pair of ventral strands. The authors created a new genus *Hidakanthus* on the basis of their single specimen. Externally *Keraocarpon* differs from *Hidakanthus* with longitudinally compressed floral head and with short, strongly falcate follicles in the latter.

In addition we could not make a detailed comparison of *Keraocarpon* with *Hidakanthus*, because in the latter no seeds are preserved in the follicle, and printed scales were omitted in all photographic figures (see Nishida *et al.*, 1996, Figures 2-13).

***Keraocarpon yasujii* Ohana, Kimura and Chitaley, sp. nov.**

Figures 1A, 2, 3, 4

Unnamed magnolialean flower with apocarpous follicles in Ohana and Kimura, 1987 p. 175, figures 1A-J.

Specimen.—INH-020 (holotype).

Locality.—Kumaoizawa (roughly 142°27'E, 42°42'N), Mikasa City, Hokkaido.

Horizon.—Coniacian-Santonian, Upper Yezo Group.

Etymology.—After Yasuji Kera, collector of the holotype.

Specific diagnosis.—Aggregate fruits large-sized. Receptacle slightly convex, disk-like. Follicles around 470, helically arranged; each follicle 2.4 cm long and 2.0 mm wide. Seeds numerous, 21-24 in each follicle.

Description.—Peduncle: The preserved part is 2.2 cm long and 1.2 cm or more in diameter (Figure 2-2A) consisting of a parenchymatous central pith, 5.0 mm in diameter, surrounded by collateral vascular bundles, 1.7 mm each, and cortex, about 1.7 mm wide. The vascular bundles are arranged concentrically, and include secondary xylem with scalariform vessels, and annular or pitted tracheids. The outer cortex consists mainly of sclerenchymatous cells which are in vertical ribs about 10 rows deep (Figure 2-3, arrows; Figure 4-7). Large cells (possibly resin cells) elliptical in cross section, 0.5 mm in major diameter, are scattered in the cortex; lining cells are not observed (Figure 4-7).

Receptacle: The receptacle is disk-like, slightly convex centrally, 2.7 cm in diameter and more than 6.5 mm thick, consisting mainly of parenchymatous cells and a number of slender fibrous bundles running vertically and horizontally (Figure 2-2B; Figure 4-8, 9).

Follicles: The follicles are numerous and helically arranged (Figure 2-2D; Figure 2-5, 6). Parastichy is uncertain, because nearly half of aggregate fruits is missing. The estimated number of follicles is 470 or fewer. The follicles

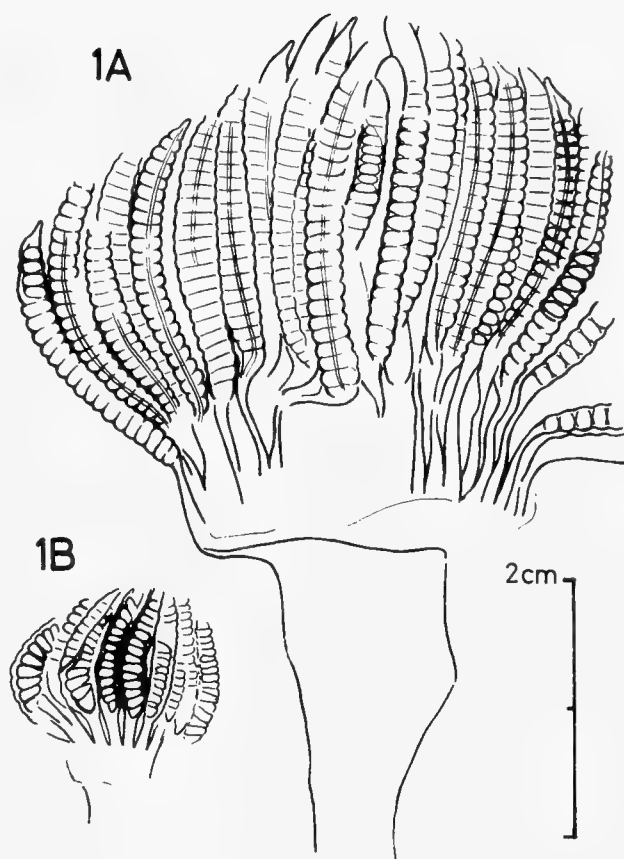


Figure 1. Longitudinally broken fruits. **1A**: *Keraocarpon yasujii* Ohana, Kimura and Chitaley, gen. et sp. nov. Drawn from Figure 2-1 (holotype). **1B**: *Keraocarpon masatoshii* Ohana, Kimura and Chitaley, sp. nov. Drawn from Figure 5-1 (holotype).

are apocarpous and conduplicate, typically 2.4 cm long and 2.0 mm wide (Figure 2-2), and circular or oblong, 1.5-2.0 mm in diameter, in transverse section (Figures 2-5, 6; Figure 3-5). Terminal of follicle with obtuse end is polygonal in transverse section (Figure 3-4). Wall of follicle consists of outer and inner layers and has a distinct adaxial median suture which is flanked on either side by a ridge, 150 μ m high, forming an adaxial crest pair with minor projections (Figure 3-5). Each follicle has a single abaxial vascular bundle (Figure 2-5, 6; Figure 3-5). A pair of bundles is present in the adaxial crest. In addition, subordinate lateral bundles are present on the outer layer of the follicle wall (Figure 3-5). Spine-like projections are observed on the outer surface of inner follicles where walls are thinner (Figure 2-6).

Stalks: Each follicle has a stalk, 6.0-8.0 mm long and 0.6 mm in diameter (Figure 2-2C; penetrates inside). In longitudinal section, this stalk is inserted into the receptacle (Figure 3-1). In transverse section, it has a large central pith, collateral bundles, and thin inner and thick outer cortices (Figures 3-3, 4). The bundles consist of vascular elements with scalariform thickenings (Figures 4-4, 5, 6).

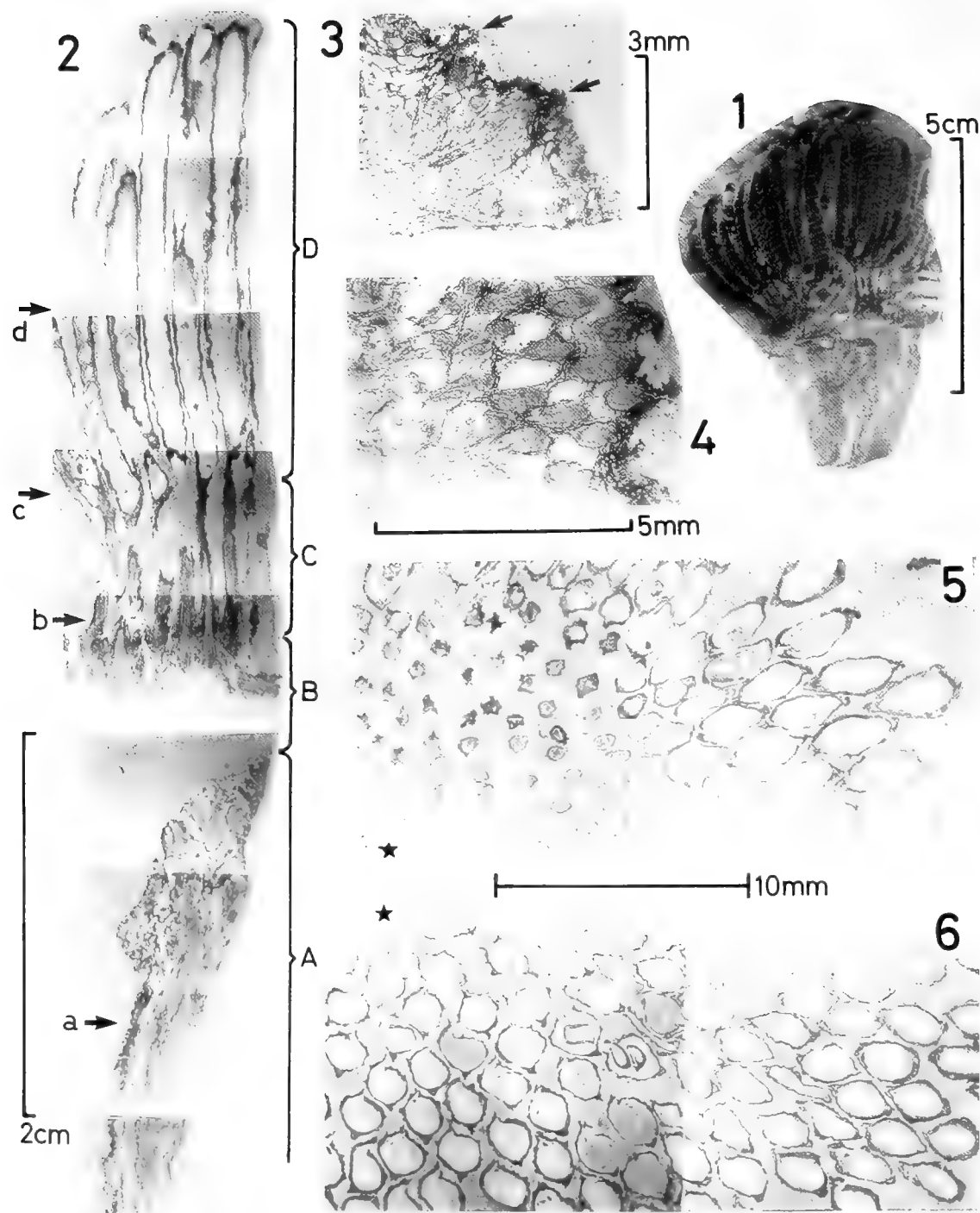


Figure 2. *Keraocarpion yasujii* Ohana, Kimura and Chitaley, gen. et sp. nov. **1.** A permineralized fruit (holotype). Its counter part is missing. **2.** A nearly radial longitudinal section of peduncle (A), poorly preserved receptacle (B), stalk of follicles (C) and apocarpous follicles (D). Surface of receptacle is slightly convex (composite photographs). **3.** A part of a transverse section of the peduncle, cut at 'a'-level in Figure 2-2 showing two sclerenchymatous ribs (arrows). **4.** Transverse section cut slightly above the receptacle (at 'b'-level in Figure 2-2). Vacant areas show the spaces among the proximal parts of stalks. **5.** Transverse section cut at 'c' level in Figure 2-2, showing proximal parts of follicles (right side) and stalks (left side). In this section, stalks (C) correspond to the convex centre of receptacle. Centre of this fruit in this section is marked by the star. **6.** Transverse section of follicles each with adaxial suture, cut at 'd'-level in Figure 2-2. The centre of this fruit in this section is also indicated by a star.

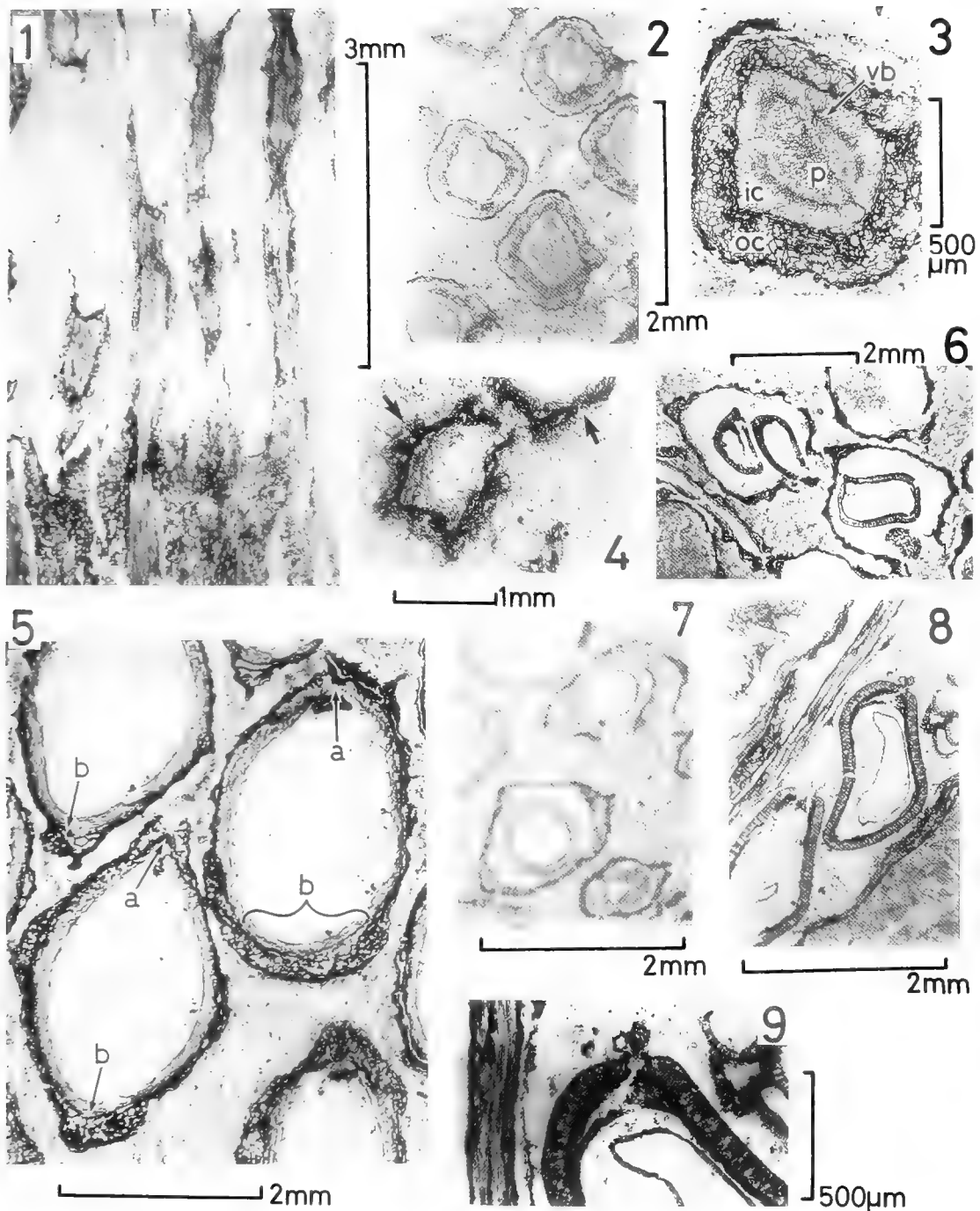


Figure 3. *Keraocarpon yasuii*, Ohana, Kimura and Chitaley, gen. et sp. nov. 1. Longitudinal section of stalks. 2. Transverse section of stalks. 3. Enlarged from Figure 3-2. Each stalk consists of thick outer cortex (oc) with large cells and oil-glands, inner cortex (ic) with small cells, vascular bundle (vb) and pith (p). Pith cells are similar to those of inner cortex. Cells of outer cortex are similar to those of receptacle. 4. Transverse section of apical parts of two follicles (arrows). Seeds are absent. 5. Transverse section of middle part of follicles with adaxial sutures facing upper side (arrow a), and abaxial thick bundles (arrow b). Two thin layers are seen in the transverse section of follicle walls. 6. Transverse section of middle part of follicles with remains of seed coats inside. 7. Transverse section of proximal part of follicles, showing the follicle walls and seed coats. 8. Longitudinal section of a follicle with two thick seed coats. 9. A thick seed coat, enlarged from Figure 3-8.

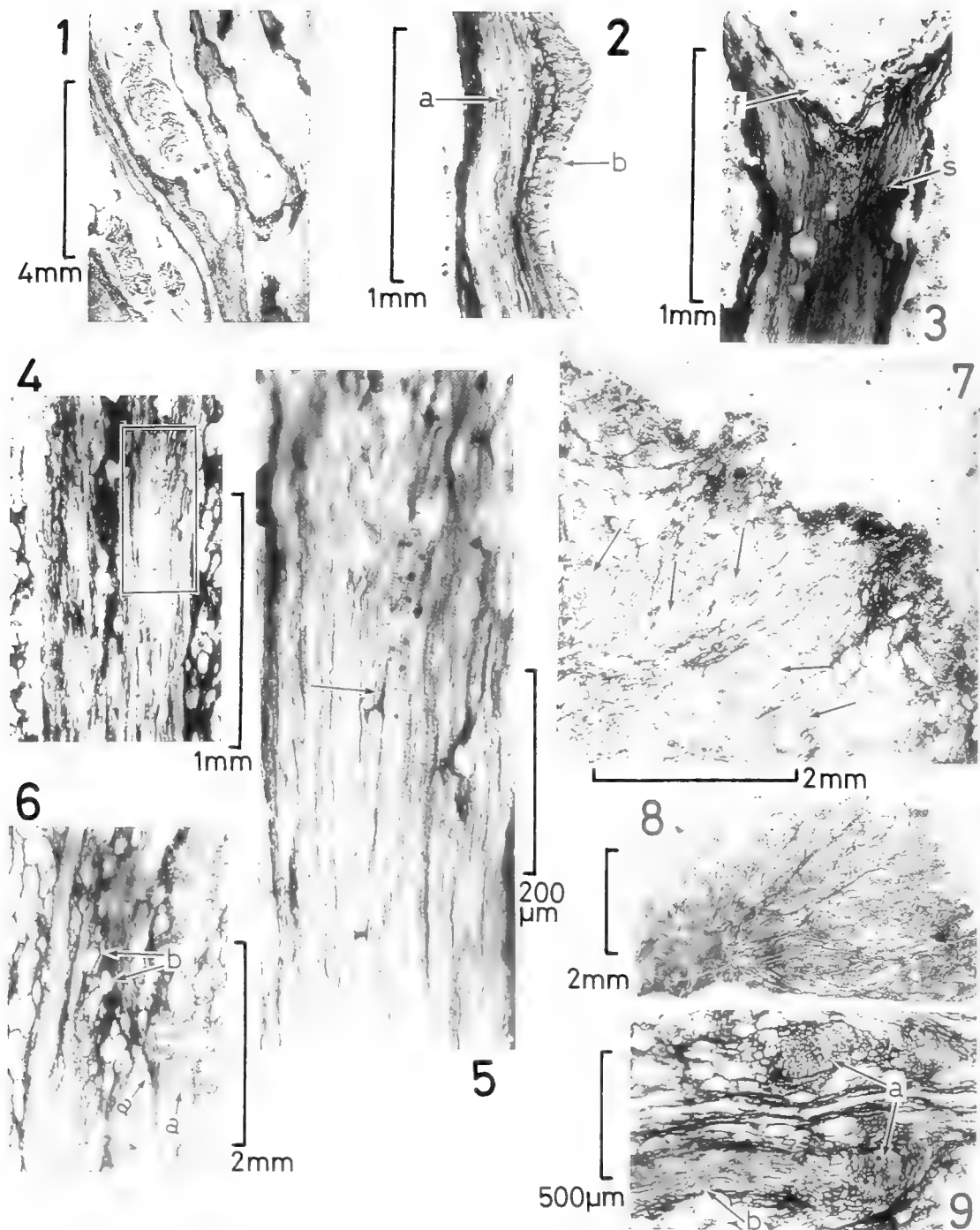


Figure 4. *Keraocarpus yasujii* Ohana, Kimura and Chitaley, gen. et sp. nov. **1.** Longitudinal section of proximal part of follicles, each with disintegrated seeds. **2.** Longitudinal section of the follicle wall (outer layer; arrow a, inner layer; arrow b). **3.** Longitudinal section of a stalk (arrow s) and the base of follicle chamber (arrow f). **4.** Longitudinal section of an enlarged stalk, showing scalariform bundles. **5.** Enlarged from the boxed area of Figure 4-4. Scalariform bundles are clearly seen (arrow). **6.** Tangential section of basal part of peduncle with eustele bundles (arrow a), showing the alternation of bundles and parenchymatous tissues (including oil glands) (arrow b). Pith is located to the right side. Phloem is not preserved. **7.** Transverse section of the basal part of peduncle, enlarged from Figure 2-3. Arrows indicate the eustele bundles. **8.** Transverse section of a part of receptacle, showing fibrous and crowded bundles. **9.** Enlarged from a part of Figure 4-8, showing vertically (arrow a) and horizontally oriented (arrow b) bundles.

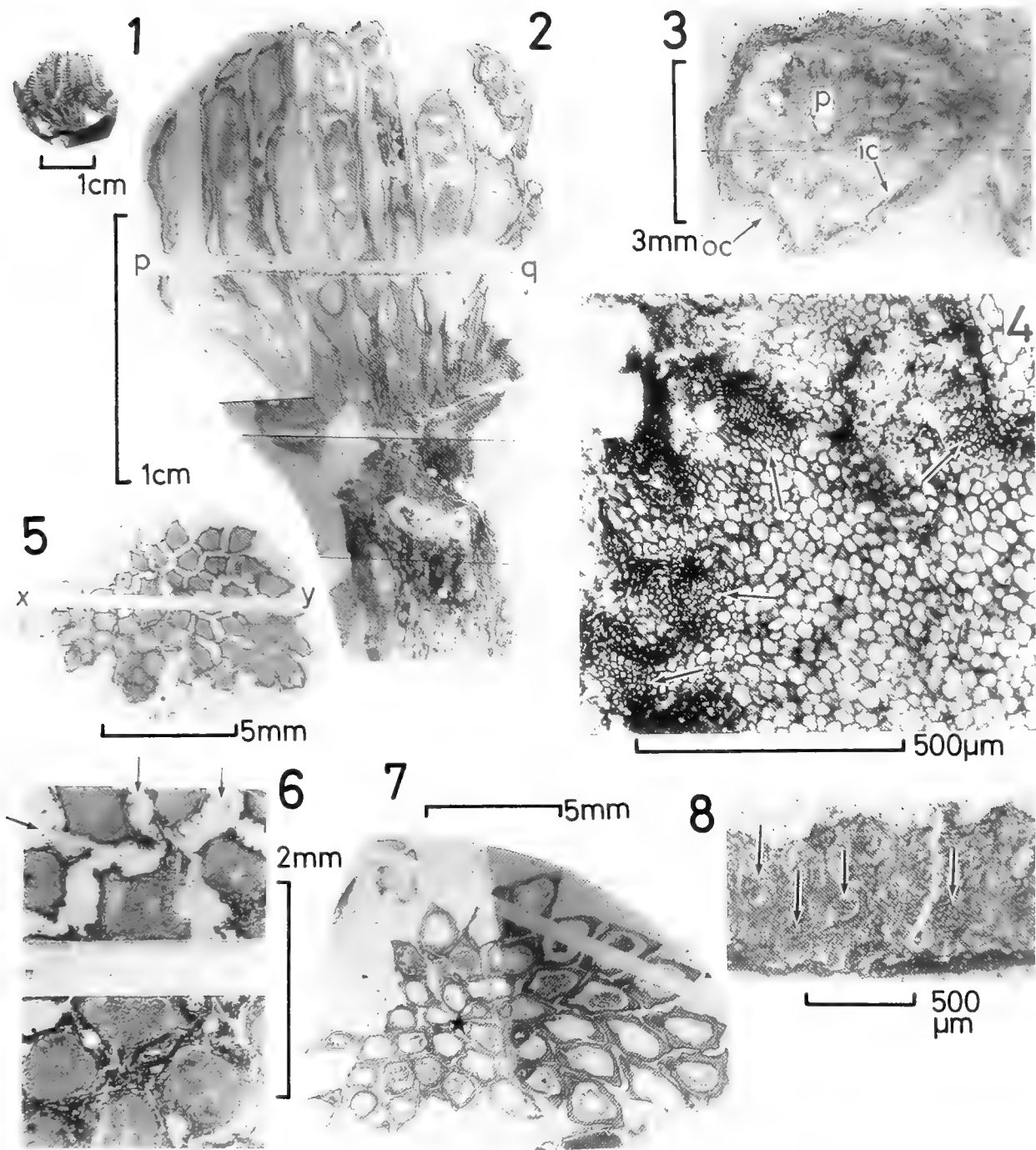
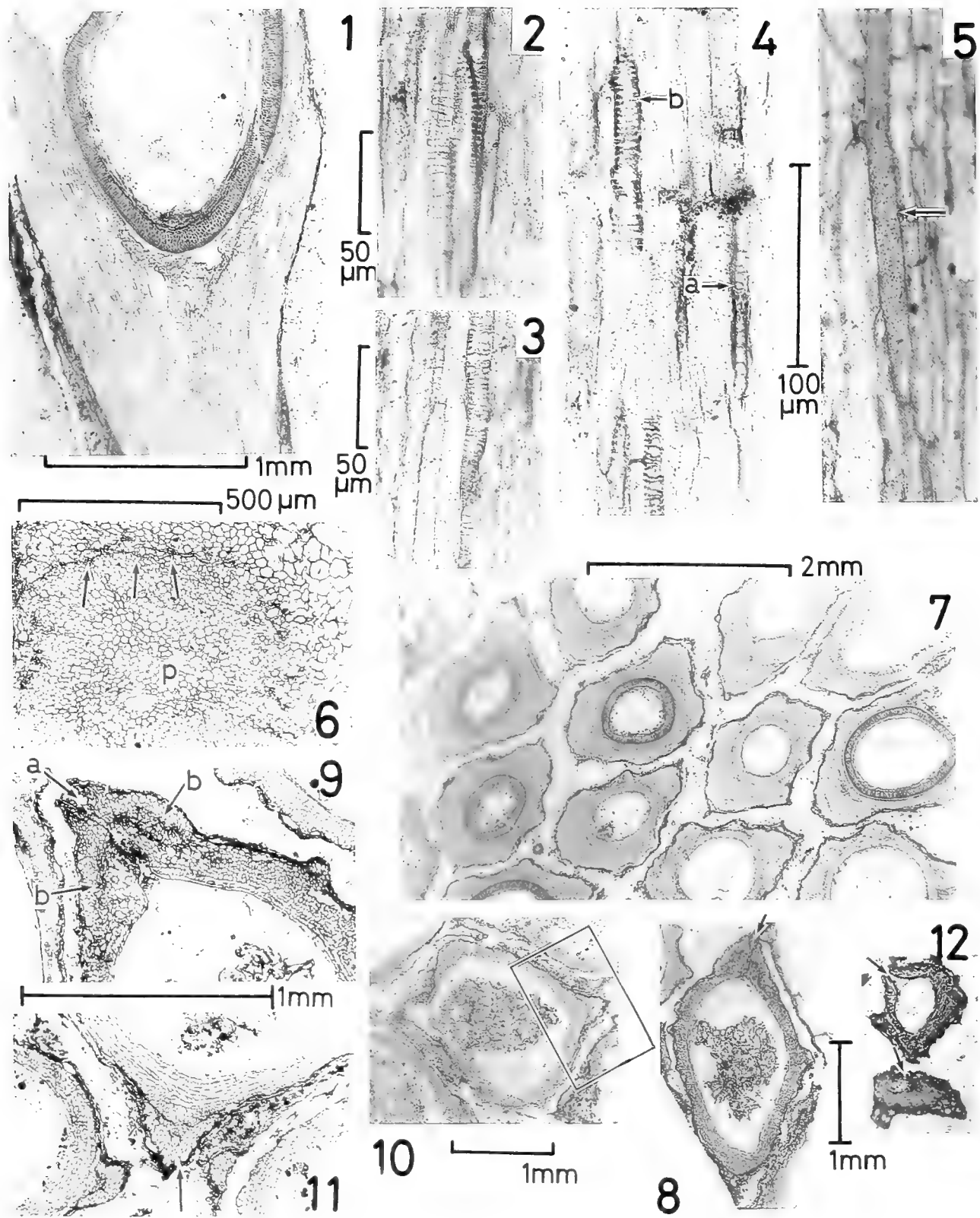


Figure 5. *Keraocarpon masatoshii*, Ohana, Kimura and Chitaley, sp. nov. **1.** Preserved parts of small aggregate fruit (holotype; compare with *Keraocarpon yasujii* shown in Figure 2-1). **2.** Radial longitudinal section of an aggregate fruit, consisting of poorly preserved peduncle, receptacle and apocarpous follicles each with distinct stalk. **3.** Transverse section of peduncle, showing large pith (p), collateral vascular bundles, inner cortex (ic) and thick outer cortex (oc). **4.** Enlarged from Figure 5-3, showing pith and collateral vascular bundles (arrows). **5.** Transverse section of stalks. x-y; zone lost by cutting (using a 0.4-mm-thick saw). **6.** Enlarged from Figure 5-5, showing polygonal or irregular outline of stalks. Arrows indicate openings filled with rock matrix. **7.** Transverse section of apocarpous follicles. Wall thickness varies according to the cutting plane. The adaxial suture faces the supposed centre of the fruit (star). **8.** Tangential section of edge of receptacle, showing horizontal vascular bundles (arrows).



Seeds: The follicle is unilocular with seeds alternately arranged in two rows, 21–24 in number in each follicle (Figure 3–6–9). Seed coat is thick with micropyle facing the adaxial suture of the follicle (Figure 3–6–9).

Keraocarpion masatoshii Ohana, Kimura and Chitaley, sp. nov.

Figures 1B, 5, 6

Specimen.—INH-021 (Holotype).

Locality.—Upper course of the Ikushunbetsu River bank, Mikasa City (4 km south of the Kumaoizawa locality where *Keraocarpion yasujii* was collected.)

Horizon.—Same as *K. yasujii*.

Etymology.—After Masatoshi Kera, collector of the holotype.

Specific diagnosis.—An aggregate fruit of follicles, small. Receptacle slightly convex. Number of follicles around 70. Stalk and wall of follicle thick. Seeds in each follicle, 15–18.

Description.—Preserved parts of this fruit are a permineralized peduncle, receptacle and apocarpous conduplicate follicles (Figures 1B, 5–1).

Peduncle: Peduncle is 5.5 mm in diameter, consisting of pith, collateral vascular bundles and cortex (Figure 5–2–4).

Receptacle: Receptacle is slightly convex disk-like, 1.0 cm in diameter and 3.5 mm thick.

Follicles: The follicles are helically arranged; their estimated number is 70. Since half of them are missing, the parastichy is uncertain. The follicles are apocarpous and conduplicate, 1.1 cm long, with transverse section circular or sometimes polygonal, 1.5–2.0 mm in diameter (Figure 5–7).

Stalk: 1.0–1.5 mm long and 0.8–1 mm thick, and is inserted into the receptacle to a depth of about 1.8 mm (Figure 5–2). It is circular to polygonal in transverse section, having a pith, vascular bundles and cortex (Figure 5–5, 6). The bundles consist of scalariform vessels and pitted tracheids (Figure 6–

1–5). The follicles are adaxially sutured (Figure 5–7; Figure 6–7–10). The follicle wall consists of two layers of cells, the outer thick and the inner thin. In each follicle, a thick vascular bundle is on the abaxial side, and a pair of adaxial bundles are on either side of the suture. No suture is observed at the proximal part of the follicle (Figure 6–7). Most of the sutures are not fully open, suggesting that its seeds are not fully matured.

Seeds: Seeds are 15–18 in number in each follicle. The seed coat is of two layers (Figure 6–1, 7). There is almost no space between the seed and the inner wall of the follicle.

Remarks.—This species is distinguished from *K. yasujii*, the type species of *Keraocarpion*, by the smaller sizes of peduncle, receptacle, and follicle and the smaller numbers of follicles, and seeds in each follicle. The transverse section of follicle is not rhomboidal as illustrated by Nishida *et al.* (1996) in their *Hidakanthus*, but elliptical or polygonal (in this work). In both fruits no male organs or other vegetative parts have been found in organic connection.

The Upper Yezo Group of marine origin contains many varied type of fossil plants. It is, however, difficult to get entire or nearly entire plant specimens, because these terrestrial plants were disaggregated in the course of taphonomy.

Acknowledgements

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← **Figure 6.** *Keraocarpion masatoshii* Ohana, Kimura and Chitaley, sp. nov. **1.** Longitudinal section of a thick stalk. Its upward extension forms follicle wall to wrap a proximal seed. No adaxial suture is present below the position of the proximal seed. **2.** Scalariform vessels in the stalk enlarged from Figure 6–1. Some perforation plate of vessels are scalariform. **3.** Same, enlarged from Figure 6–1. **4.** An annular tracheid (arrow a) and scalariform vessels (arrow b) in stalk enlarged from Figure 6–1. **5.** Pitted tracheid. Pits are in two rows (arrow) enlarged from Figure 6–1. **6.** Transverse section of proximal part of a stalk, showing pith (p) and small collateral bundles (arrows). **7.** Transverse section of follicles, cut along the p–q line in Figure 5–2, showing thick and irregularly formed follicle walls. **8.** Transverse section cut along the middle part of a marginal follicle. Follicle is transversely rhomboidal and the seed is disintegrated. The position of the adaxial suture is indicated by an arrow. **9.** Transverse section of a follicle cut slightly above the section as in Figure 6–8, showing adaxial suture (arrow a). The vascular bundles are seen at each crest (arrow b). **10.** Transverse section of a central follicle, cut at the same level as in Figure 6–8, showing the wall. **11.** Enlarged from the boxed area of Figure 6–10, showing the abaxial bundle (arrow) and thick-layered follicle wall. **12.** Transverse section of apical part of two follicles with distinct adaxial sutures (arrows). The walls are irregular in form.

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行 事 予 定

- ㊟第149回例会は、2000年6月23日(土)から24日(日)に「群馬県立自然史博物館」で開催されます。一般講演の申し込み締切は2000年5月4日です。
- ㊟第150回例会(2001年1月下旬開催予定)には、「茨城県自然博物館」から開催申し込みがありました。2001年年会・総会は、21世紀最初の年会ですので、東京大学と国立科学博物館共催でシンポジウムを中心とした形式で開催を企画しています。現在常務委員会で開催形式を検討中です。ご意見があれば行事係までお寄せ下さい。
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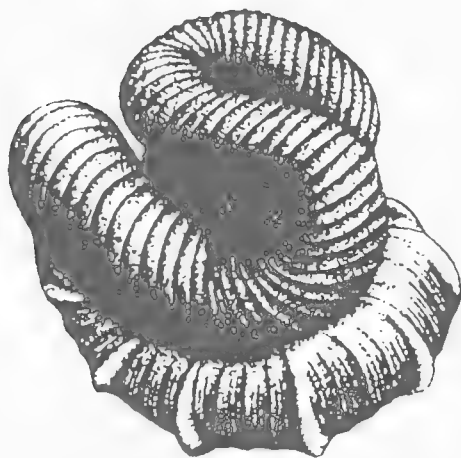
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Cover: Idealized sketch of *Nipponites mirabilis* Yabe, a Late Cretaceous (Turonian) nostoceratid ammonite. Various reconstructions of the mode of life of this species have been proposed, because of its curiously meandering shell form (after T. Okamoto, 1988).

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Recognition of breeding populations in foraminifera: an example using the genus *Glabratella*

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Abstract. Four morphospecies of foraminifera, *Glabratella opercularis*, *G. subopercularis*, *G. nakamurai*, and *G. patelliformis*, all of which have similar test morphologies, were reclassified by the use of both morphological characters and interbreeding experiments. Because specimens of *Glabratella* have been shown to reproduce sexually, it should be possible to determine breeding populational boundaries within *Glabratella* and to compare these with morphologically based taxonomic boundaries.

Using stable characters, three morphogroups were reclassified from the four morphospecies. Laboratory interbreeding experiments revealed that individuals belonging to the same morphogroup formed gamontogamous pairs and then reproduced. However, individuals belonging to different morphogroups did not produce any gamontogamous pairs. This indicates that each of the reclassified morphogroups represents a distinct breeding population.

Within the same morphogroup, individuals collected from two different localities closer than 100 km apart could interbreed with each other. However, individuals from more than 500 km apart could not breed with each other, even though the morphological characters of the individuals were very similar. This suggests that the population structure of the *P. opercularis* morphogroup is very similar to those of ring species.

Key words: benthic foraminifera, breeding populations, interbreeding experiments, morphospecies, ring species

Introduction

Conventionally, the species-level systematics of foraminifera have been carried out only with morphological characters of the test. Recently, biogeographic data, indicating areal and depth distributions in the sea, have also been used for defining foraminiferal species in addition to morphological data (e. g., Matoba, 1970). Fifty or sixty thousand foraminiferal morphospecies, both modern and extinct ones, have been described (Bock *et al.*, 1985; Loeblich and Tappan, 1988; Culver, 1993). However, doubt remains whether or not foraminiferal species defined by test morphologies are equivalent to breeding populations that can interbreed within a morphologically defined population (Boltovskoy and Wright, 1976).

According to the definition of Mayr (1969), a species is the array of populations that are actually or potentially able to interbreed and that are reproductively isolated from other such arrays under natural conditions. This definition is mainly appropriate for metazoan taxa with two sexes, and it is problematic to adopt this concept to protistan taxa, which have both sexual and asexual reproduction during their life cycles.

How should we define species among protistan taxa?

Sonneborn (1957) discussed the species concept in Protista. He carried out breeding experiments within a *Paramecium* species complex that enabled him to recognize breeding populations that could form conjugation pairs. He called this “breeding population” a “syngen”. A “syngen” may be comparable to a “species”. However, there still exists much controversy about the nature of species in protistan taxa, in particular foraminifera (Boltovskoy, 1954; Grell, 1959; Nyholm, 1961; Schnitker, 1974; Tendal, 1990).

In this study, as a first step toward solving the species problem in foraminifera, we have examined whether morphologically based species have the same boundaries as breeding populations for foraminifera. Breeding populations of *Glabratella* can be recognized rather easily, because specimens of this genus have been observed participating in sexual reproduction through formation of gamontogamous pairs (Myers, 1943). Observation of sexual reproduction is a positive method for determining the degree to which populations interbreed in foraminifera.

Sixteen morphospecies of *Glabratella* are known from the sea adjacent to the Japanese Islands (Matoba, 1970;

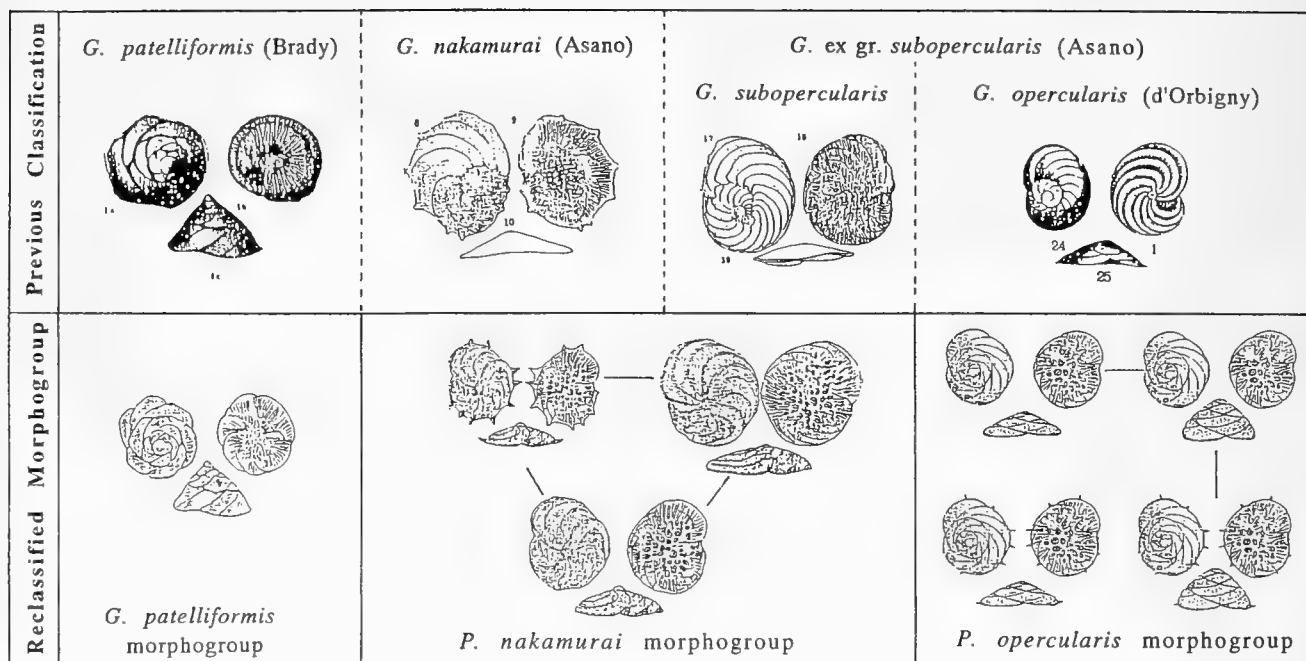


Figure 1. Four selected morphospecies of *Glabratella* that exhibit similar test morphologies. Original illustrations are shown in the upper panel. Reclassified morphogroups are shown in the lower panel. Not to the scale.

Kanesaki, 1987MS). Most of them live in the intertidal zone of rocky shores. They crawl on leaves or thalli of seaweeds and graze microalgae or organic detritus on the surface of seaweeds (Kitazato, 1984, 1988, 1994). Among these *Glabratella* species, *G. nakamurai* (Asano), *G. opercularis* (d'Orbigny), *G. patelliformis* (Brady), and *G. subopercularis* (Asano) have similar test morphologies (Figure 1). Some specimens have mixed morphological characters of two species. Thus, it is sometimes difficult to identify specimens at the species level. In this study, we tried to reclassify these four morphospecies by making use of both morphological characters and the results of interbreeding experiments in the laboratory.

Methods of study

Samples for the study were collected from the intertidal zone of rocky shores adjacent to the Japanese Islands (Kanesaki, 1987MS). Living individuals were collected at tide pools in Omaezaki Cape (34°36'N, 138°14'E) and Shimoda Bay (34°39'N, 138°57'E), both in Shizuoka Prefecture, central Japan. Additional samples were collected at tide pools in Oshika Peninsula, Miyagi Prefecture (36°15.0'N, 136°08.4'E) and Echizen-Matsushima Coast, Fukui Prefecture (38°23.9'N, 141°24.7'E) for interbreeding experiments among different localities. Sampling localities are shown in Figure 2.

Two approaches were used during the course of this study. Firstly, we carefully observed the ontogeny of test morphologies of *Glabratella* morphospecies, both of agamont and gamont specimens, using a scanning electron

microscope.

Secondly, culture experiments were carried out to examine the breeding ability of reclassified morphogroups. Seaweed with attached living foraminifera was collected from tide pools and placed in large culture tanks filled with well oxygenated sea water (Kitazato, 1984, 1988). Living foraminifera were transferred from the culture tank into a small petri dish for observation under a binocular microscope.

Individuals were cultured in petri dishes. A diatom species, *Navicula* sp., was isolated from the tide pool of the Omaezaki Cape, cultured, and used as a food source. *Glabratella* spp. ate little of other single-celled algae such as *Chlorella* and *Dunaliella* (Chlorophyceae), *Amphiprora* (Diatomophyceae) and *Cryptomonas* (Cryptophyceae) species.

Both intraspecific and interpopulational breeding experiments were carried out using a small petri dish. Two individuals, each collected from a different locality or different morphogroup, were placed on a small petri dish (28mm inner diameter) with fresh seawater. The formation of a gamontogamous pair was observed in the petri dish using a phase-contrast apparatus attached to an inverted microscope (Nikon-TMD Cultivation Microscope System and Olympus IMT-2 Inverted Microscope System). An automatic microphotographic system (Nikon-HFM) attached to the inverted microscope was used to record the process of gamontogamy. Interspecific breeding experiments by three morphospecies were carried out using a large petri dish (87mm inner diameter). Twenty gamont individuals of the three morphogroups were mixed in a petri dish and ob-

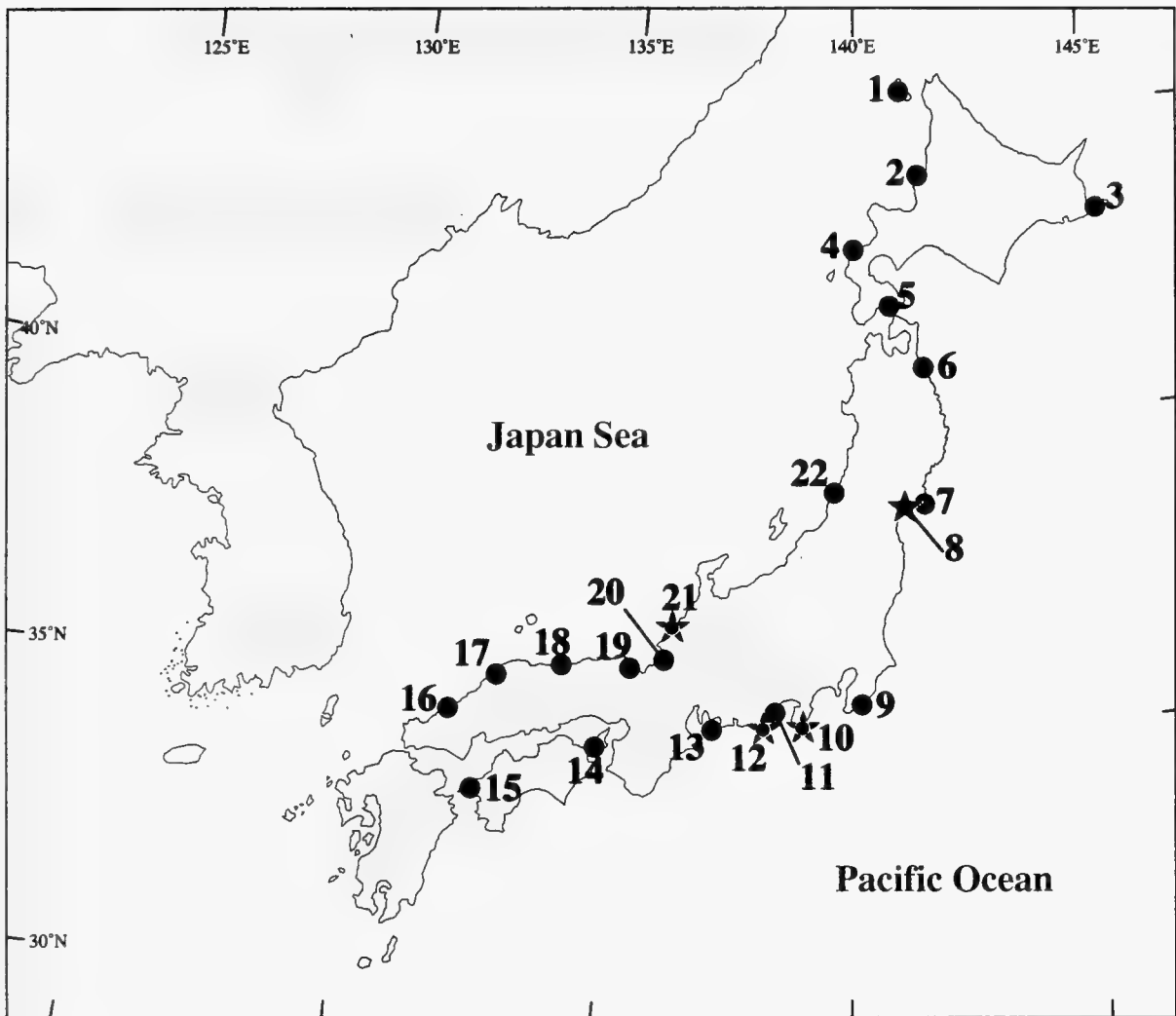


Figure 2. Map showing sampling localities. Closed circles indicate localities for measuring height/diameter ratio of *Planoglabratella opercularis* morphogroup. Asterisks are localities where interpopulational breeding experiments were carried out. 1. Rebuntou. 2. Rumoi. 3. Nokamappu. 4. Biya. 5. Kattoshimisaki. 6. Hachinohe. 7. Hamagurihama. 8. Oshika Peninsula (Sendai Bay). 9. Kamogawa-Bentenjima. 10. Shimoda (Ooura). 11. Obama. 12. Omaezaki. 13. Irakomisaki. 14. Yoroizaki. 15. Takaura. 16. Tsuchida. 17. Futamata. 18. Nagawase. 19. Momojima-Nishi. 20. Hayase. 21. Echizen-Matsushima. 22. Kobato.

served almost continually until individuals formed gamontogamous pairs. It is easy to distinguish specific morphogroups under a binocular microscope.

Results and discussion

Morphological observations

Glabratella species have trochospiral, spiroconvex, and conical tests. The umbilical side is flattened with a slightly depressed umbilicus. The surface of the spiral side is rugose. The umbilical side is ornamented with rows of pustules that form radially aligned striae. Sutures are flush with the surface on the spiral side in general, but depressed on the umbilical side. The aperture opens at the interiomarginal part of the ventral side of the ultimate chamber of the

test. The aperture is an arched slit that is bordered by a weakly developed rim. Radial striae, which form groove and ridge systems, are developed on the ventral face. Radial striae probably have a function related to rhizopodial activity during movement or feeding (Kitazato, 1992).

These morphological characters are common to all four morphospecies. They are also common to both agamont and gamont individuals, although the test size of the agamont is about twice as large as that of the gamont.

Several kinds of sculpture on the ventral side of the test, such as tubercles, radial granules, and crenulation of the suture line between chambers, together with surface relief and basic chamber shapes, are stable during ontogeny in each morphogroup (Figure 3). We tried to reclassify *Glabratella* morphospecies into several morphotypes using

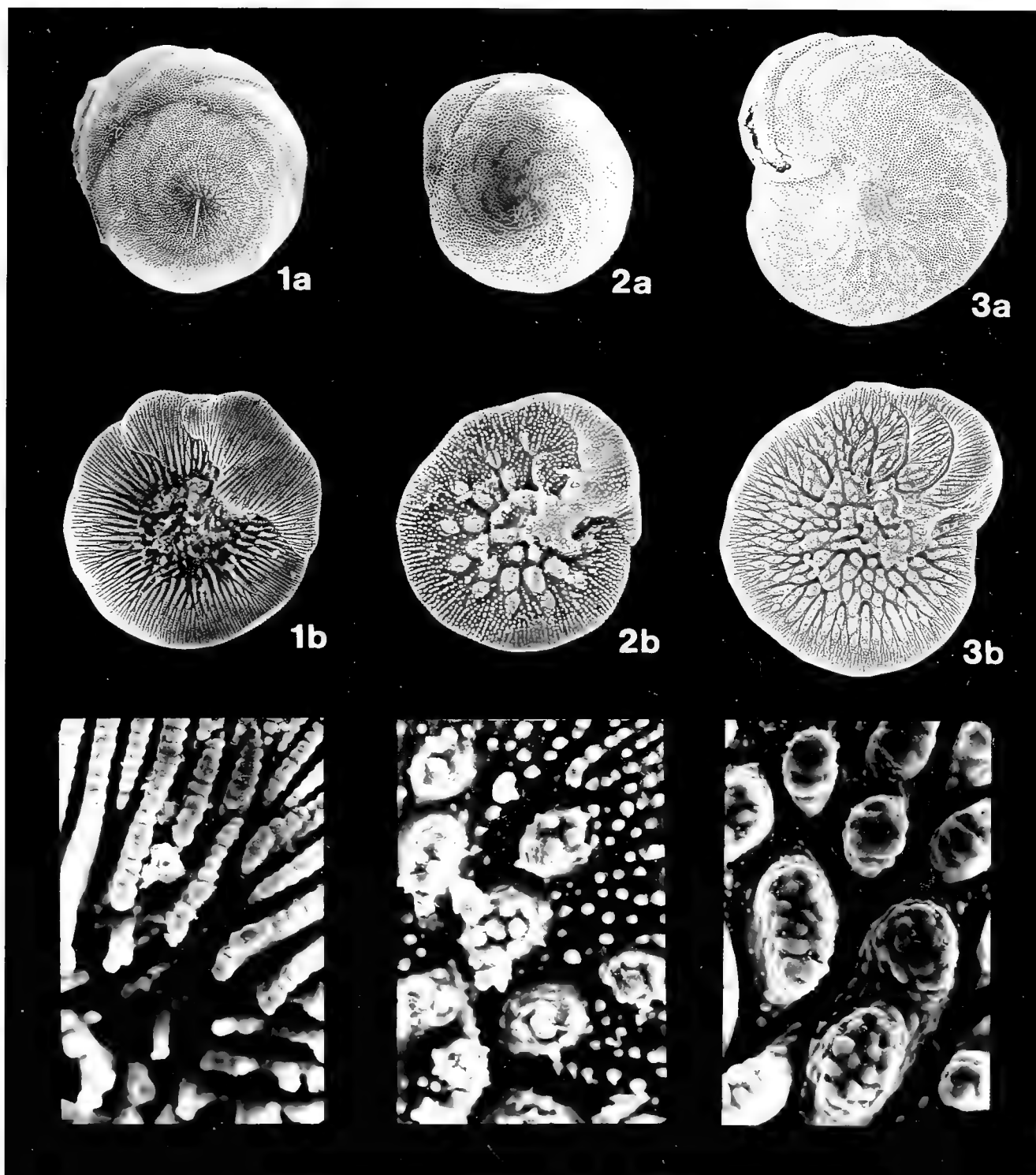


Figure 3. Overview of test morphologies of three morphogroups of the genus *Glabratella*. Dorsal (a) and ventral (b) views and enlargement of ventral surface (c) are shown for 1–4. **1a c.** *Glabratella patelliformis* morphogroup. **1a.** $\times 94$. **1b.** $\times 94$. **1c.** $\times 540$. **2a c.** *Planoglabratella opercularis* morphogroup. **2a.** $\times 94$. **2b.** $\times 94$. **2c.** $\times 540$. **3a c.** *Planoglabratella nakamurai* morphogroup. **3a.** $\times 86$. **3b.** $\times 78$. **3c.** $\times 600$.

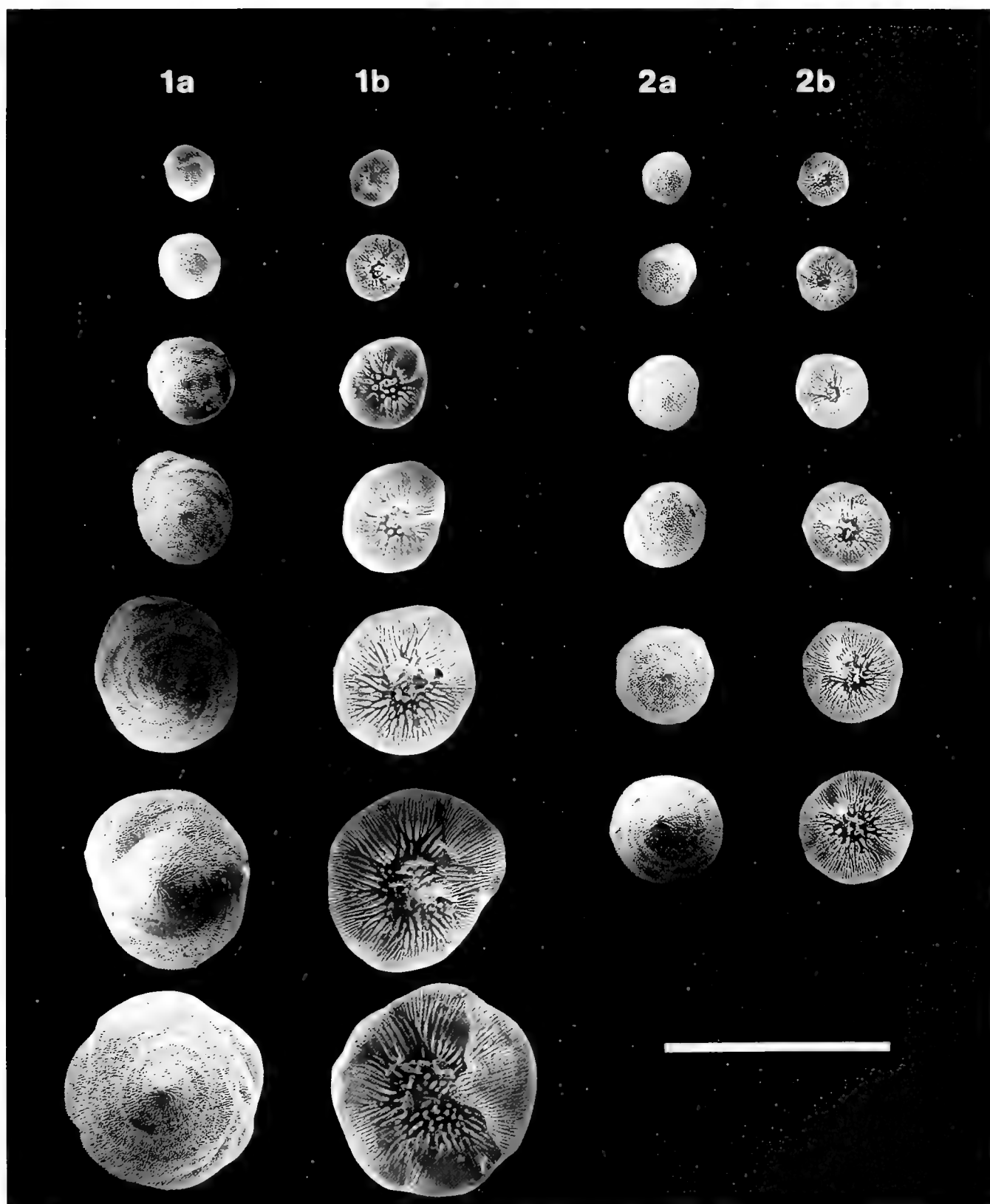


Figure 4.

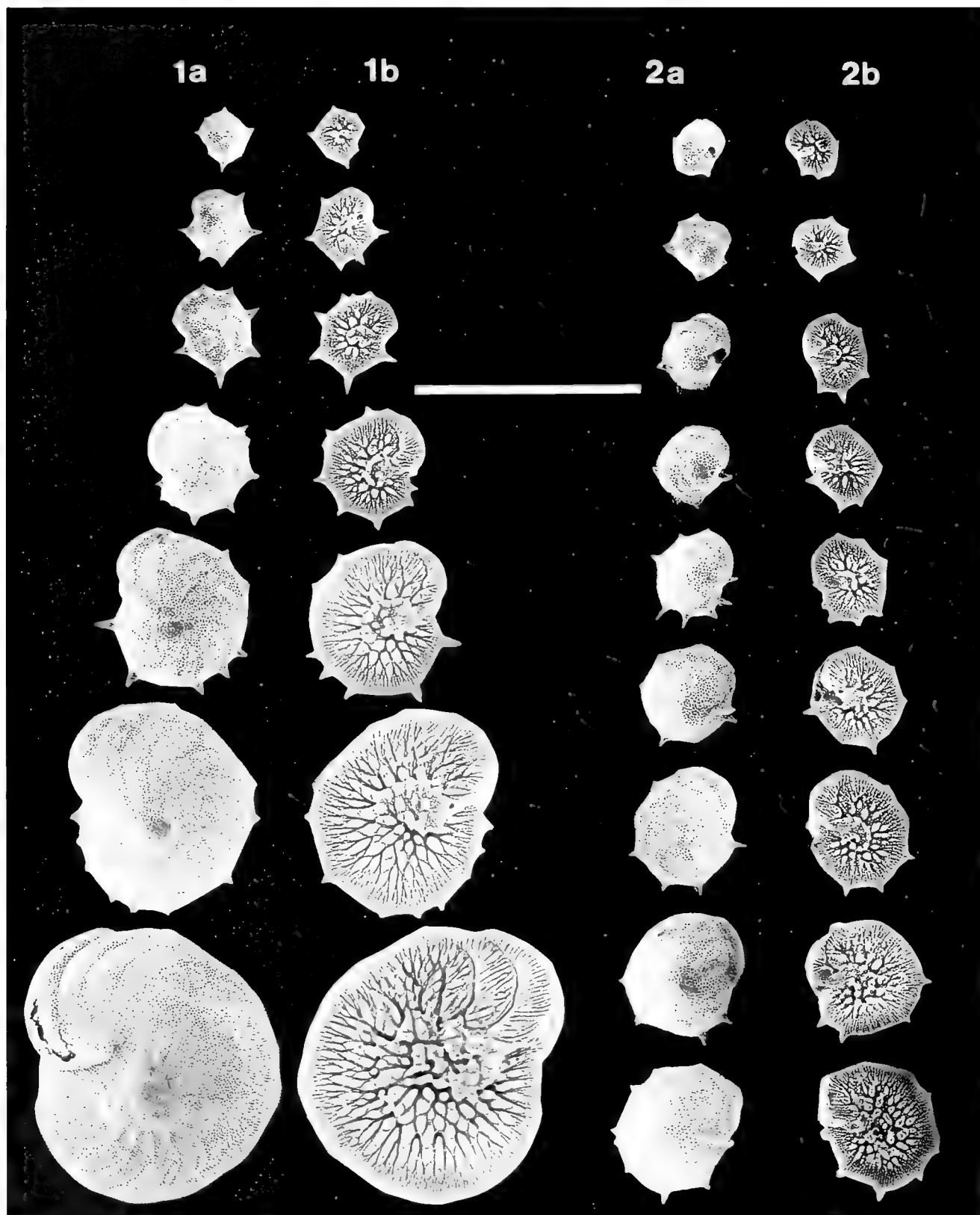


Figure 5.

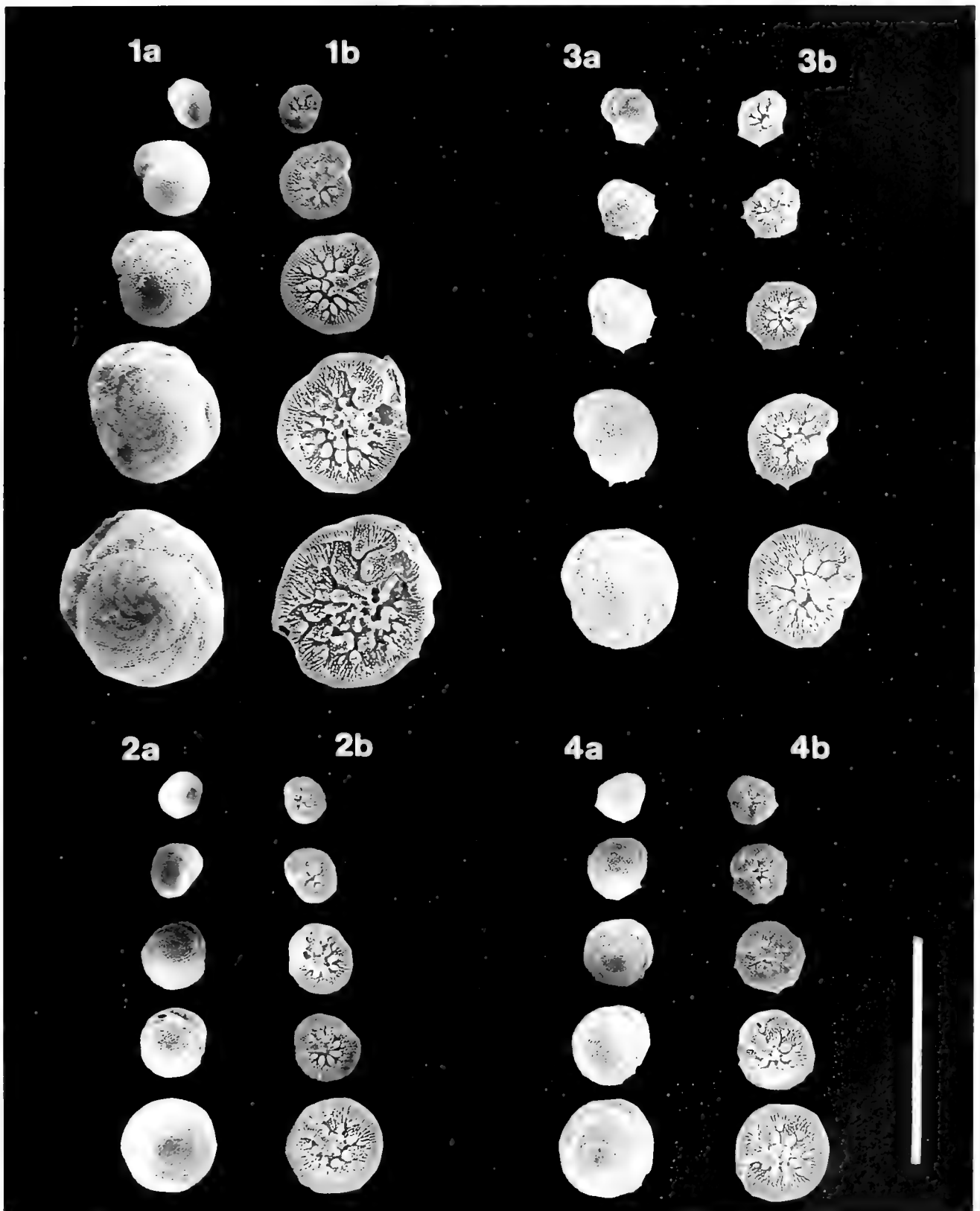


Figure 6.

only these stable morphological characters.

The four morphospecies were reclassified into three morphogroups (Figure 1). The characters of each reclassified morphogroup are as follows.

i) *Glabratella patelliformis* morphogroup (= *Discorbina patelliformis* Brady, 1884): This morphogroup is characterized by a strongly crenulated suture line between chambers, radial ridges made from a straight arrangement of needles, and needlelike tubercles at the center of the ventral side (Figure 3.1a–c).

ii) *Planoglabratella opercularis* morphogroup (= *Discorbis opercularis* d'Orbigny, 1839): This one is characterized by having rather smooth suture lines in comparison to *G. patelliformis*, sparsely arranged radial ridges, and spiny tubercles on the central area of the ventral side (Figure 3.2 a–c). Recently, Loeblich and Tappan (1988) separated flat *Glabratella* species from genus *Glabratella*, and established *Planoglabratella* as a new generic name. Here, we apply the new generic name to *G. nakamurai* and *G. opercularis*, following Loeblich and Tappan (1988).

iii) *Planoglabratella nakamurai* morphogroup (= *Discorbis nakamurai* Asano, 1951): This morphogroup is characterized by simple bowl-like sutures, radial ridges only at the peripheral part of the ventral side, and tough flamboidal tubercles that cover most of the ventral surface (Figure 3.3a–c).

These morphological characters are present continuously through all growth-stages within the same morphogroup (Figures 4–6). These characters are also continuously present in both gamont and agamont tests, even though gamont and agamont test sizes are different.

Several morphological characters such as peripheral spines, height/diameter (=H/D) ratio and others vary with growth and also with the ambient environment. Peripheral spines of *P. nakamurai* disappeared in later growth stages, becoming covered by nonspinose chambers (Figure 5). The involutely coiled whorl in *P. nakamurai* sometimes becomes evolute at maturity. The mature stage of *P. nakamurai* is quite similar to the holotype of *G. subopercularis* (Asano). Thus, we regard *G. subopercularis* as a junior synonym of *P. nakamurai*.

The height/diameter ratio of the test of *P. opercularis* varies from locality to locality. The H/D ratio of populations in the Japan Sea was higher than in the Pacific (Figure 7). The H/D ratio at each locality was calculated from the slope of linear regression of height against diameter from one population. One hundred specimens were measured at

each locality. Along the Pacific, a population from Omaezaki Cape showed a higher mean H/D ratio than one from Ooura in Shimoda Bay (Figure 7). The H/D ratio also varied seasonally (Figure 8). The difference in H/D ratios of allopatric populations was larger than the seasonal fluctuations at one locality.

Like *P. nakamurai*, there are both spinose and nonspinose individuals of *P. opercularis* (Figure 6). However, peripheral spines of this morphogroup appeared at all ontogenetic stages (Figure 6.3, 6.4). This phenomenon was not observed in *P. nakamurai*. This morphological variation in *P. opercularis* also appeared in all localities around the Japanese Islands. Geographic variation in the proportion of spinose and nonspinose individuals in individual populations has not yet been analyzed.

Interbreeding experiments

Interbreeding experiments were carried out among three morphogroups that were reclassified based on morphological characters to examine whether or not these morphogroups represented interbreeding populations. Interbreeding experiments were also made among populations of *P. opercularis*, which are distributed in remote localities along the Japanese Islands.

Formation of a gamontogamous pair progressed as follows (Figure 9):

- 1) When two individuals came near enough to reach each other by rhizopodia, they immediately extruded a bundle of rhizopodia between them (Figure 9.1).
- 2) They maintained contact via these bundles for a few minutes, but the tests remained at some distance from each other (Figure 9.1).
- 3) After a few minutes they pulled each other until their tests touched (Figure 9.2, 9.3).
- 4) Still connected by the bundles, they lifted their tests and stuck themselves together along their ventral sides (Figure 9.4–9.8). Subsequently, most of the rhizopodia were withdrawn into the paired tests. To form a gamontogamous pair took approximately one hour on average. The exchange of gametes took place directly between the pair. We could not directly observe exchange of gametes between a pair through the tests, because *Glabratella* tests are too thick-walled and thus not transparent enough. Two-chambered agamontic juveniles appeared outside the pair one or two days after pair formation.

The processes of constructing a gamontogamous pair in

Figure 4. 1–2. Ontogeny of both agamont and gamont of *Glabratella patelliformis* (Brady). Collected at Omaezaki Cape, Shizuoka Prefecture. Scale bar indicates 500 μ m. **1a.** Dorsal view of agamont. **1b.** Ventral view of agamont. **2a.** Dorsal view of gamont. **2b.** Ventral view of gamont.

Figure 5. 1–2. Ontogeny of both agamont and gamont of *Planoglabratella nakamurai* (Asano). Collected at Hayama, Kanagawa Prefecture. Scale bar indicates 500 μ m. **1a.** Dorsal view of agamont. **1b.** Ventral view of agamont. **2a.** Dorsal view of gamont. **2b.** Ventral view of gamont.

Figure 6. 1–4. Ontogeny of *Planoglabratella opercularis* (d'Orbigny) both with and without peripheral spines. From Omaezaki Cape, Shizuoka Prefecture. Scale bar indicates 500 μ m. Dorsal (a) and ventral (b) views are shown for 1–4. **1a.** Agamont individuals without peripheral spines. **1b.** Agamont individuals without peripheral spines. **2a.** Gamont individuals without peripheral spines. **2b.** Gamont individuals without peripheral spines. **3a.** Agamont individuals with peripheral spines. **3b.** Agamont individuals with peripheral spines. **4a.** Gamont individuals with peripheral spines. **4b.** Gamont individuals with peripheral spines.

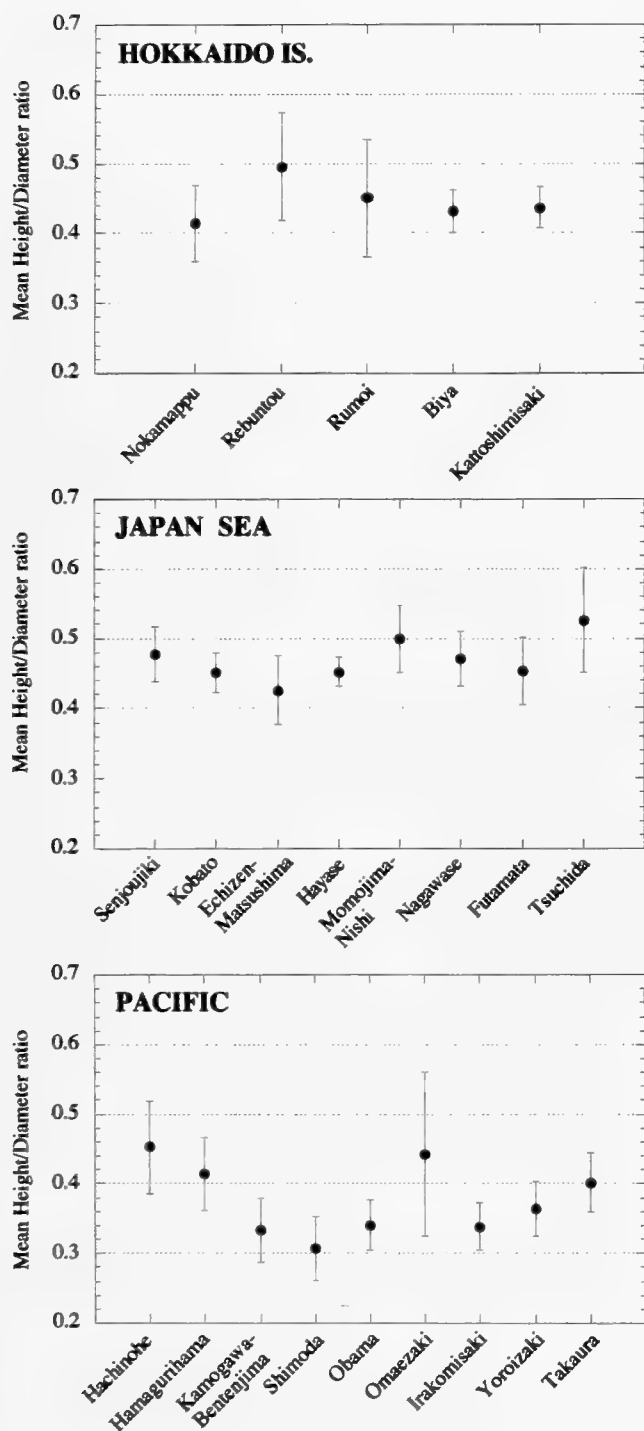


Figure 7. Geographic distributions of height/diameter ratio of *Planoglabratella opercularis* morphogroup around the Japanese Islands from various samples taken during different seasons. Black circles mark average height/diameter ratio at different localities. Bars straddling circles indicate the range of one standard deviation of data at each locality.

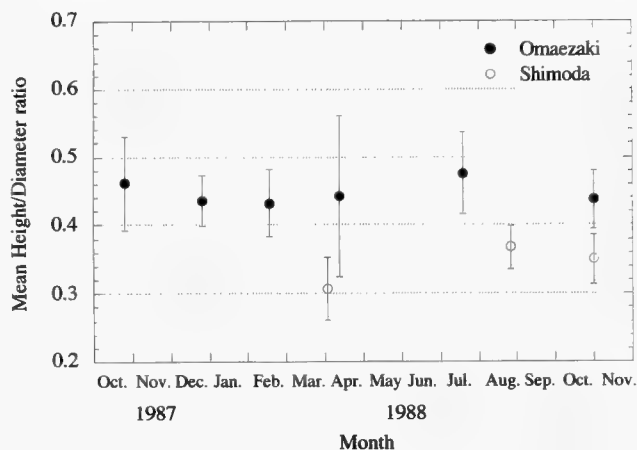


Figure 8. Seasonal differences of average height/diameter ratios of *Planoglabratella opercularis* both at Omaezaki Cape and Shimoda Bay, in Shizuoka Prefecture. Black circles show the data from Omaezaki Cape. Open circles show the data from Shimoda Bay. Bars indicate the range of one standard deviation of data at each locality.

Glabratella are mostly the same as those described by Le Calvez (1950) for *Discorbis mediterraneus*.

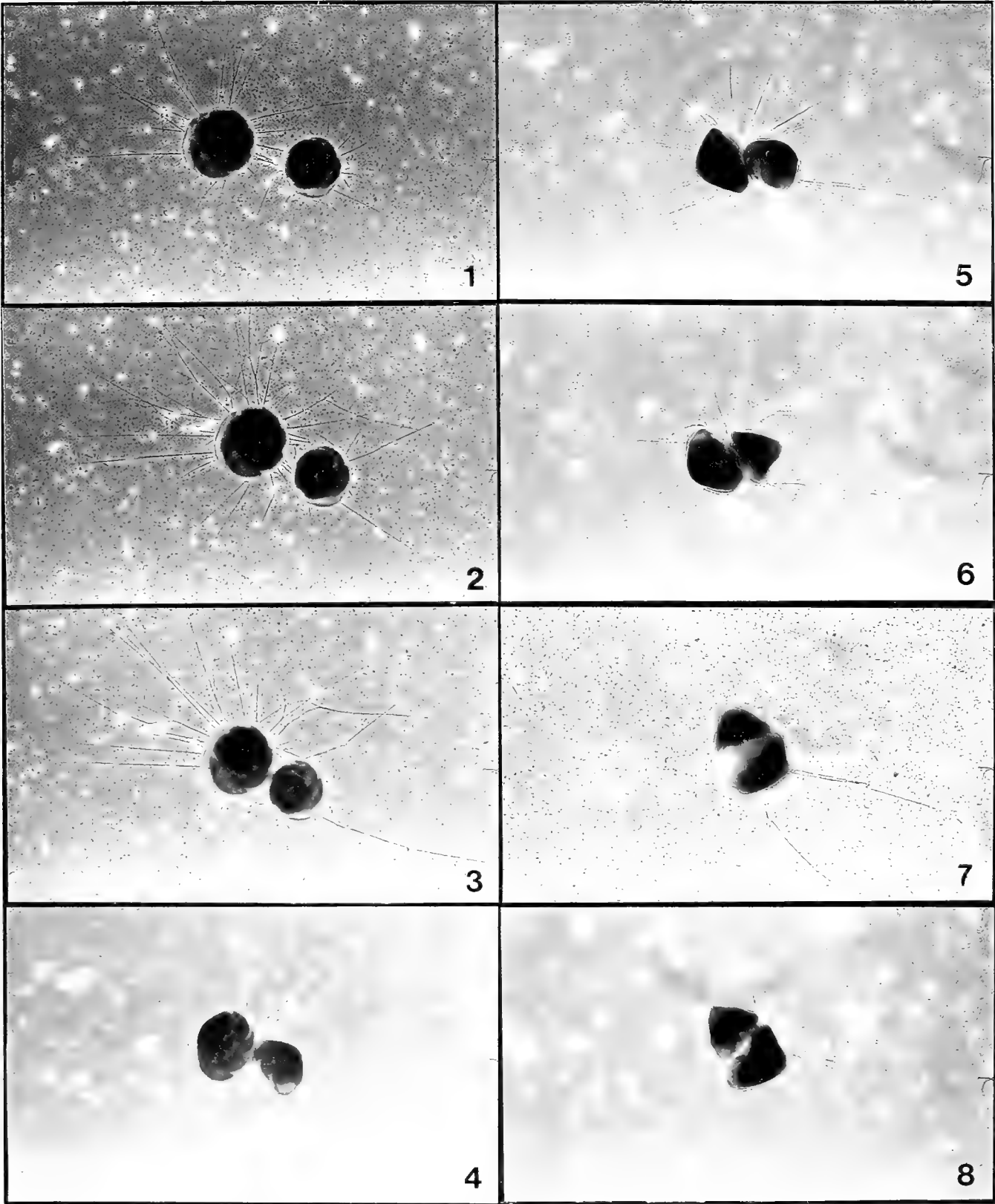
The results of the interbreeding experiments are summarized in Figure 10. Individuals that belonged to the same morphogroup mated, but those that belonged to separate morphogroups did not (Figure 10A). These results suggest that the species reclassified by morphology can probably be considered to be breeding populations.

However, there are individuals within the same population of a morphogroup that did not mate. Although they touched each other, they did not go further in forming a pair; instead, the rhizopods were disconnected and the individuals moved independently. The results indicate that some kinds of sexual differentiation may exist in *Glabratella*, as suggested by Le Calvez (1950), Grell (1957, 1958a, b, 1959), Weber (1965) and Berthold (1971) for several species that formed gamontogamous aggregates during fertilization.

Gamont individuals from the same parental agamont sometimes formed pairs; however, there was no exchange of gametes. This could mean that autogamy may not occur in *Glabratella*, even though autogamy has been found among species of the genus *Rotaliella* as described in Grell (1973).

Individuals from different morphogroups never reacted to each other, even if their rhizopodia were close enough to touch.

As described above, two morphological variations occur in *P. opercularis*, i. e., presence/absence of peripheral spines and height/diameter ratio. Both individuals with and without peripheral spines were able to form gamontogamous pairs and reproduced during culture experiments (Figure 10B). SEM photographs of a gamontogamous pair formed by a spinose and a nonspinose individual are shown in Figure 11. Both high and low trochospiral individuals also formed gamontogamous pairs (Figures 10B, 12.1, 12.2) and also re-



A INTERSPECIFIC BREEDING EXPERIMENTS

| | <i>P. nakamurai</i> | <i>P. opercularis</i> | <i>G. patelliformis</i> |
|-------------------------|---------------------|-----------------------|-------------------------|
| <i>P. nakamurai</i> | 7/18 | 0/48 | 0/22 |
| <i>P. opercularis</i> | | 11/30 | 0/33 |
| <i>G. patelliformis</i> | | | 1/4 |

B INTRASPECIFIC BREEDING EXPERIMENTS*Planoglabratella opercularis* (d'Orbigny)

| | spinose | non-spinose | high H/D ratio | low H/D ratio |
|----------------|---------|-------------|----------------|---------------|
| spinose | 2/3 | 7/9 | *** | *** |
| non-spinose | | 35/58 | *** | *** |
| high H/D ratio | | | 11/30 | 9/14 |
| low H/D ratio | | | | 47/73 |

C INTERPOPULATIONAL BREEDING EXPERIMENTS*Planoglabratella opercularis* (d'Orbigny)

| | Echizen-Matsushima | Oshika Peninsula | Shimoda | Omaezaki |
|--------------------|--------------------|------------------|---------|----------|
| Echizen-Matsushima | 1/3 | *** | *** | 0/3 |
| Oshika Peninsula | | 2/6 | *** | 0/6 |
| Shimoda | | | 47/73 | 10/61 |
| Omaezaki | | | | 16/41 |

Figure 10. Results of interbreeding experiments with both inter- and intraspecific populations. Results of interpopulational breeding experiments are also shown. Numerals to the left of the slash show combinations that actually formed a gamontogamous pair. Numerals to the right of the slash indicate the number of experiments for each combination. ***: no experimental data.

A. Interspecific breeding experiments, B. Intraspecific breeding experiments, C. Interspecific breeding experiments.

produced (Figure 12.3, 12.4). These results clearly show that all variants belong to the same population and can interbreed. Both spines and H/D ratio were formerly used as key morphological characters for defining *Glabratella* species. We have not yet examined how these morphological characters appear in daughter or granddaughter cells.

Interbreeding experiments among *P. opercularis* populations from different localities indicate that geographically remote populations do not make gamontogamous pairs (Figures 10C, 13). Gamont specimens between Omaezaki

Cape and Shimoda Bay made gamontogamous pairs and reproduced. However, individuals between Omaezaki Cape and Oshika Peninsula, Miyagi Prefecture and between Omaezaki and Echizen-Matsushima Coast, Fukui Prefecture did not make gamontogamous pairs with each other, even though morphological characteristics of *P. opercularis* populations at the three localities are very similar. These interbreeding experiments of individuals of remotely separated populations show that the interbreeding abilities of populations are closely related to geographic distances between

Figure 9. Series of photographs showing the process of forming a gamontogamous pair of *Glabratella patelliformis* (Brady) on September 1, 1987. Photographed in 1. 1548 hours, 2. 1549 hours, 3. 1550 hours, 4. 1554 hours, 5. 1555 hours, 6. 1556 hours, 7. 1557 hours, 8. 1600 hours. Collected at Shimoda Bay, Shizuoka Prefecture.

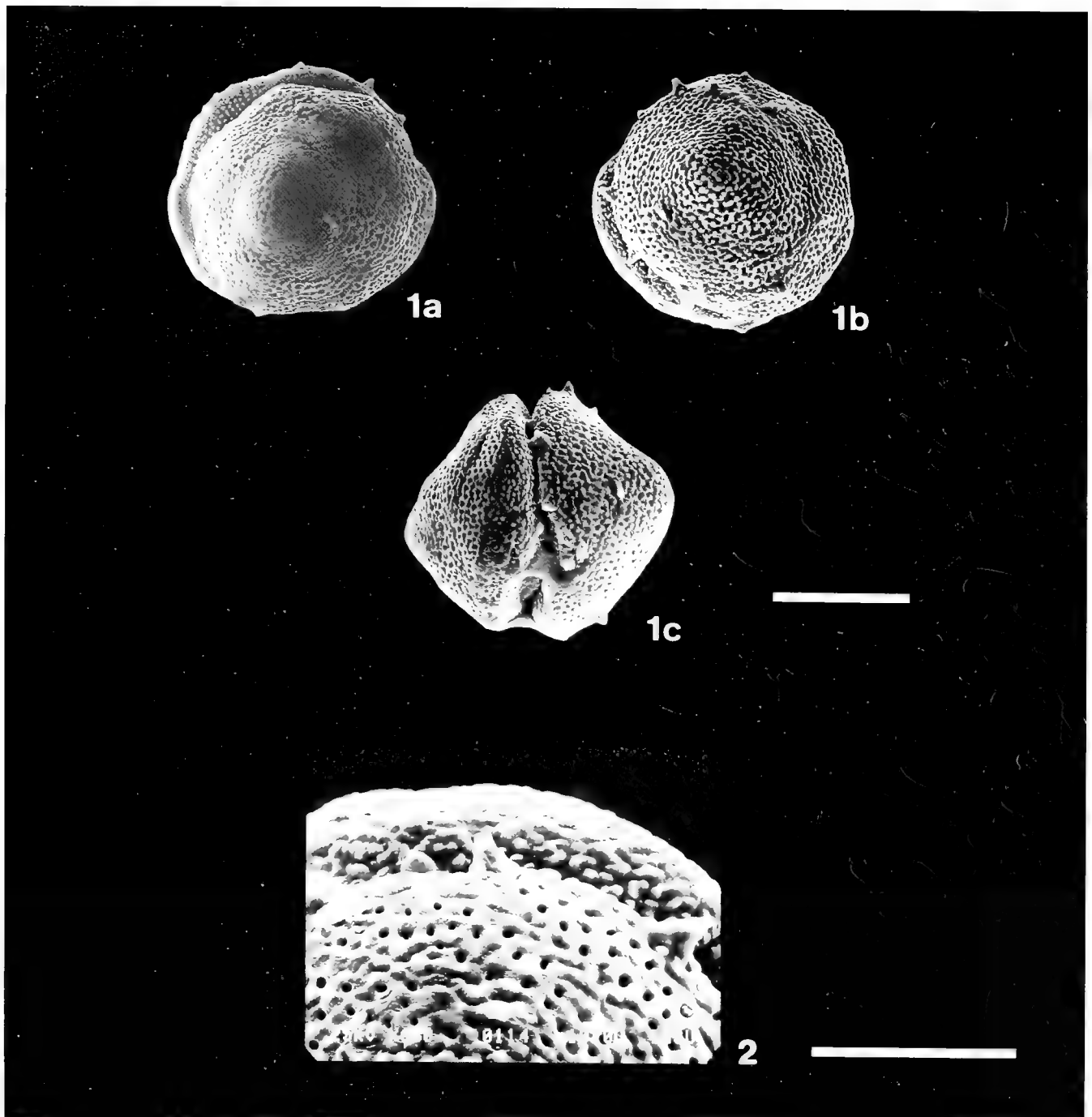


Figure 11. Gamontogamous pair between individuals with peripheral spines and without spines of *Planoglabratella opercularis* (d'Orbigny). Scale bars for 1 a, b, c and for 2 indicate 100 μ m and 50 μ m respectively. 1a. Specimen without peripheral spines, 1b. Specimens with peripheral spines. 1c. Side view of gamontogamous pair. 2. Enlargement of peripheral spines.

Figure 12. Photographs showing the reproductive process of *Planoglabratella opercularis* (d'Orbigny) from a gamontogamous pair during culture experiments. 1. Gamontogamous pair between individual showing high height/diameter ratio of Omaezaki population and individual showing low height/diameter ratio of Shimoda population. Agamont juveniles are visible within one pair. Photographed at 2130 hours, November 4, 1988. 2. Side view of gamontogamous pair. Upper right individual shows higher height/diameter ratio than that of lower left individual. Photographed on November 4, 1988, 2140 hours. 3. Spreading of agamont offspring from the parental pair. Photographed on November 5, 1988. Juvenile agamonts have two chambers when they leave. 4. Juvenile agamont individuals with three chambers. Photographed on November 7, 1988.

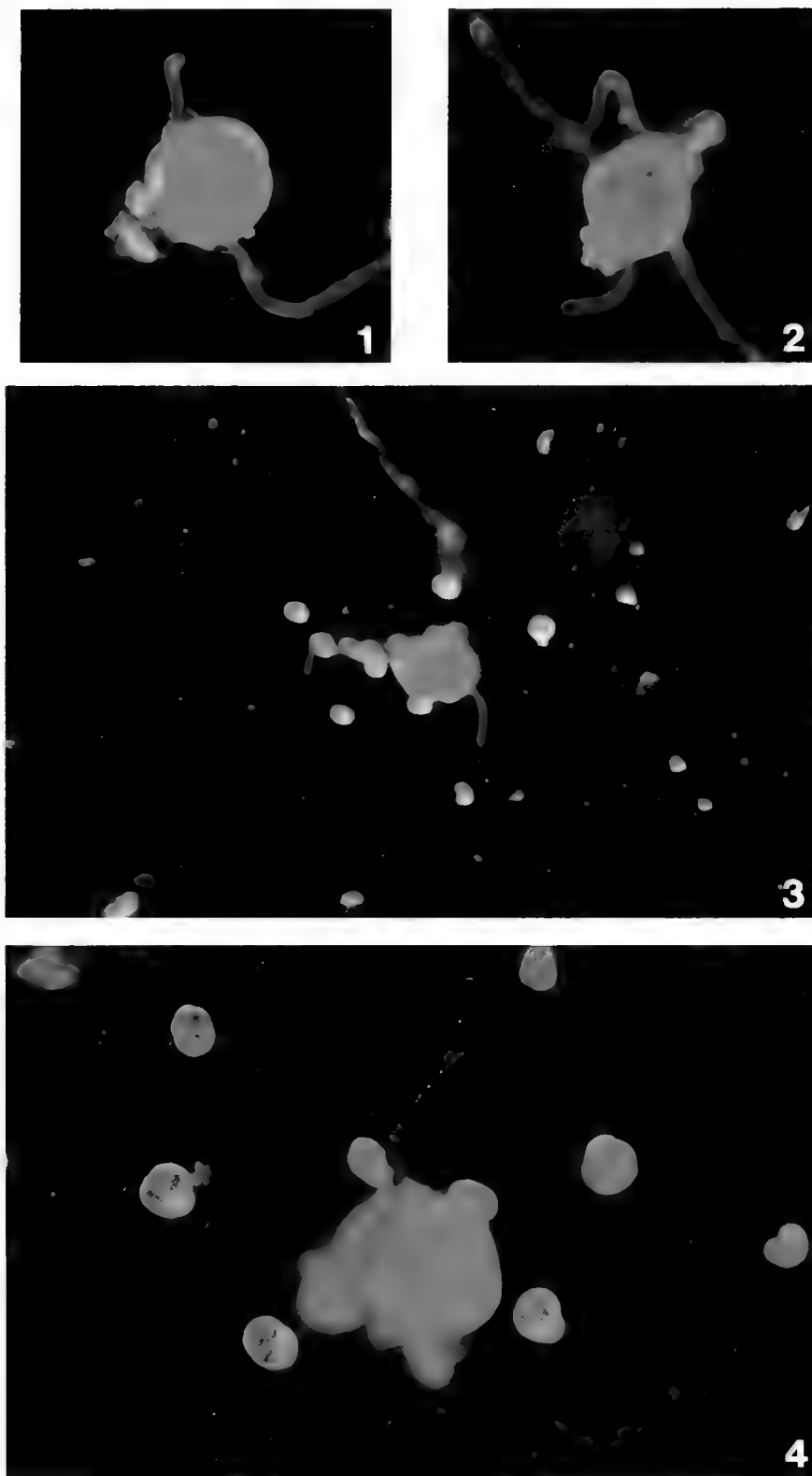


Figure 12.

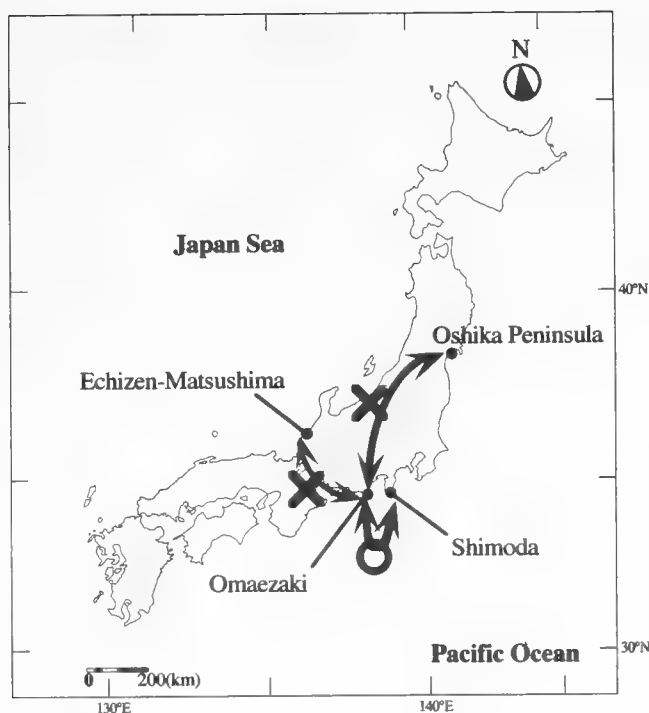


Figure 13. Results of interbreeding experiments of individuals among geographically remote populations. Map shows localities from which individuals actually tried to interbreed. Circle and cross marks in the figure refer the populations that can and cannot interbreed, respectively. The results show that individuals from proximate localities can interbreed.

them. Individuals that succeeded in interbreeding belong to proximate populations. For instance, Omaezaki Cape is only 100 km from Shimoda Bay at the closest distance along the shoreline. In contrast, individuals from distant localities failed to interbreed. Oshika Peninsula is about 500 km from Omaezaki Cape. The Echizen-Matsushima Coast is more than 1000 km from Omaezaki Cape. Thus geographic distance is critical in determining interbreeding abilities among populations of a single morphospecies in *Glabratella*. This phenomenon suggests that populations of this glabratellan morphospecies have characteristics of ring species, with chains of local populations that can interbreed between neighboring populations.

Summary

Four *Glabratella* morphospecies were reclassified into three morphogroups, according to stable morphological characters. There are several key morphological characters that are stable with ontogenetic stages, life cycle, and/or geographic distance. Certain morphological characters changed during ontogeny. Interbreeding experiments show that reclassified morphospecies can breed within one morphogroup. Several morphological characters are not stable during ontogeny. This shows that we cannot use every morphological feature to define *Glabratella* species.

Interbreeding experiments using individuals collected from geographically remote populations demonstrate that individuals of closely located populations can breed with each other, whereas individuals from distant populations cannot interbreed. These results suggest that glabratellan populations are chains of small, reproductively isolated populations.

Interbreeding experiments are a powerful tool to elucidate populational structure of morphologically defined species in foraminifera.

Acknowledgments

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Foraminal structures of some Japanese species of the genera *Ammonia* and *Pararotalia*, family Rotaliidae (Foraminifera)

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Abstract. Rotaliid foraminifera have a complicated foraminal structure that has been recognized as the so-called toothplate. As to the interpretation of this toothplate, however, there has been confusion among foraminiferologists as to whether it is the same as the buliminid toothplate or not. In order to elucidate the apertural and foraminal structure, we examined some Japanese species of the genera *Ammonia* and *Pararotalia*.

The apertures of *Ammonia* and *Pararotalia* show fundamentally the same style of construction, but the resultant structures are different among species. We recognized two main components instead of the indefinite toothplate in the aperture: foraminal plate and umbilical coverplate. The foraminal plate constructed out of a foramen is a free structure of the bilamellar wall. This plate is originally formed in the final chamber where it delimits the posterior side of the final aperture. The umbilical coverplate closes the umbilical side of the preceding foramen. This coverplate is originally bilamellar and is continuous from the foraminal plate. Both the foraminal plate and umbilical coverplate are formed when the final chamber is constructed. The umbilical coverplate interconnects the new and preceding foraminal plate, which may lead to the original concept of toothplate. However, the umbilical coverplate is not associated with the final chamber wall, but assists in closing the umbilical side of the preceding chamber wall. Such a chamber construction is restricted to rotaliids, thus we reject the term toothplate as only indicating modified structures that pass through the aperture.

Descriptions of the rotaliid aperture are of value when we note the foraminal plate and umbilical coverplate. Thus two types of foramen, *Ammonia*-type and *Pararotalia*-type, were developed in the rotaliids.

Key words: aperture, foraminal plate, rotaliid foraminifera, taxonomy, toothplate.

Introduction

The toothplate is a characteristic structure developed in some taxa of benthic foraminifera (originally called “tooth plate”, recently “toothplate”; e. g., Loeblich and Tappan, 1964, 1987). It has a varied morphology, usually manifested as a protruded free structure passing through the aperture. Before Hofker (1950, 1951a, b) recognized this structure as a useful systematic criterion of hyaline calcareous foraminifera, various distinctive parts of the aperture were called lip, tongue, tooth, partition and flap. Hofker’s toothplate was regarded as a homologous structure with these variously named structures. Many forms having these apertural decorations have been classified into a number of families based on their apertural morphologies. Thus most hyaline calcareous foraminifera were included in Hofker’s order

Dentata (Hofker, 1951a). However, morphologically, some of these structures should be grouped together in the same category and some should be clearly differentiated from it. The toothplate concept includes so many forms of apertural complexity that rigid application of this term leads to ambiguous comparisons in systematics. In particular, the apertural complex of Hofker’s Protoforaminata, the group having protoforamen, is different from that of his Deuteroforaminata, the group having both protoforamen and deuteroforamen.

In addition to such a confused recognition of the toothplate and related structures, development of the scanning electron microscopes (SEM) permitted the lamellar structure of the toothplate to be examined. The toothplate has been recognized as a bilamellar structure consisting of an inner lining and an outer lamella (Hansen and Reiss, 1971). However, the lamellarity is not consistent, since Revets (1993)

suggested that the buliminid toothplate is made from the inner lining. Thus, the concept of toothplate is still confused among foraminiferal researchers in its structural and morphological aspects. The rotaliid toothplate is the best example of this, it being unclear whether it should be recognized as homologous with the buliminid toothplate or not on the basis of morphology and structure.

We describe the apertural and foraminal structures based on artificially dissected specimens and suggest the necessity of recognizing the morphological variation of the aperture.

Methods

Internal structure of foraminiferal test was examined by a scanning electron microscope using a hardened canada balsam (Nomura, 1983c). Some authors stress the importance of lamellar structure, particularly to the understanding of toothplate structure (e. g., Revets, 1989, 1993). In reconstructing the lamellar structure for the sectioned and etched specimens that have been embedded in epoxy resin we encountered difficulties, particularly for thinner walls. Alternatively, we etched the sectioned specimens with 0.5% phosphoric acid to observe the internal structure before removing the canada balsam. This method gives better results in interpreting the three-dimensional lamellar structures within walls.

Previous observations on the aperture of *Ammonia*

Earlier workers examined thin sections of foraminifera or examined the test with naturally broken walls to observe the toothplate. In this way, the toothplate of *Ammonia beccarii* (Linné), type species of the genus *Ammonia*, has been recognized as a free structure asymmetrically folded longitudinally and convex towards the umbilical side of the chamber (Hofker, 1950, 1951a, b; Reiss and Merling, 1958). Reiss and Merling (1958) showed various figures of the toothplate and related structures, and introduced several terms for its specific structures. They described the toothplate to "run always from the intercameral foramen towards the umbilical side for part of the way, turning through torsion towards the dorsal side at their distal ends." Thus the toothplate is convex towards the umbilical center. The rotaliid septal flap, originally proposed by Smout (1954), is also regarded by those authors as an extension of the toothplate, although they retain the term septal flap. Cifelli (1962) suggested the toothplate of *A. beccarii* was not homologous with the original toothplate and he separately called it an axial plate and a lip. He observed that the axial plate is imperforate and the umbilical extension of the plate passes into a chamber flap, without any openings into the umbilical area. The lip, in the different sense of Reiss and Merling (1958), is formed by the axial plate anteriorly projecting through the aperture at the bottom of the septum, except for the final one. Before the recognition of these apertural modifications by these workers, Ishizaki (1943) first noted the morphological difference between the aperture (as the final opening) and the foramen (as the preceding opening). However, he did not refer to any specific anatomical observations.

Based on SEM examination, Seibold (1971) recognized the axial wall as forming a different part of the toothplate in *Ammonia*. Seibold's axial wall and lip correspond to Cifelli's axial plate and chamber flap. Hansen and Reiss (1971) first introduced the concept of a foraminal plate and an umbilical coverplate instead of the toothplate for the rotaliid foraminifera, suggesting the presence of this plate in all chambers, including the final one. They interpreted the septal flap which forms not only the foraminal plate on an axial chamber wall (=previous coil), but also the umbilical coverplate, as showing a continuous lamellar structure. Their observations corroborate Reiss and Merling's explanation. The septal flap consists of an inner lining, which covers the preceding bilamellar septal wall. This lamellar model has been adopted in Lykke-Andersen (1976). Thus the foraminal plate and the coverplate are bilamellar in the original construction. They suggested that the so-called fissure and intraseptal passage are formed as an imperfect adhesion of the septal flap to the preceding chamber. They referred to this fissure as an interocular space. Müller-Merz (1980) supplied detailed anatomical information on rotaliids and she discussed the apertural structure based on the foraminal plate and cover plate (same sense of umbilical coverplate) model.

Lévy *et al.* (1986) suggested the suprageneric similarities of some rotaliids, including *Ammonia*, to discorbids. They pointed out a similarity in internal structure for which they used the term paries proximus instead of the toothplate. They describe "It (=paries proximus=toothplate) is a thin plate which divides from the septum towards the umbilical face and which constitutes an oblique groove-like fold, instead the chamber, joining the preceding coil. This plate also spreads backwards, that is, in a proximal direction, closing the edge of the folium of the preceding chamber. In equatorial section we give the name 'retroparies' to the back part of the paries proximus." Their paries proximus and the retroparies correspond to the foraminal plate and umbilical coverplate respectively. Although their proposal to subsume the rotaliids within the discorbids at the family level is rejected by Haynes and Whittaker (1990), based on ontogenetic analyses of umbilical modifications, including canals and fissures, there is a similarity in the structure of paries proximus in both taxonomic groups.

The complexity of the internal structure of *Ammonia* is reflected in these different terms. On the other hand, differing recognition of the internal structure among researchers makes for uneasy interpretations. Hottinger *et al.* (1991) redefined the toothplate, particularly in relation to that of *Pararotalia* (see below). They stressed the presence of their toothplate (s.s.) in *Pararotalia* and its absence in *Ammonia*, indicating a difference in suprageneric classification. Revets (1993) questioned whether the rotaliid toothplate was homologous to the buliminid toothplate. He mentioned "The internal structures in rotaliids are not equivalent to toothplates, rather they all seem to conform to the foraminal plate coverplate concept." His argument originated from the difference between the bilamellar structure of rotaliid walls and the single-layer inner lining origin of the buliminid toothplate. Simple usage of the toothplate thus leads to confusion among researchers. The situation is

similar in cassidulinids. Nomura (1983a, b) showed that simply the presence or absence of a toothplate is of little taxonomic value. We should describe the apertural decoration with careful attention to the various parts.

Previous observations on the aperture of *Pararotalia*

The detailed apertural structure of *Pararotalia* has been discussed by Loeblich and Tappan (1957, 1964) and Reiss and Merling (1958), based on its type species *Pararotalia inermis* (Terquem) from the Eocene of Paris Basin. Loeblich and Tappan (1987) described the aperture as interiomarginal and extraumbilical-umbilical, and the foramen as areal with the attachment of the toothplate at the proximal margin of the penultimate chamber. Loeblich and Tappan's toothplate is seemingly used in a broad sense, but they distinguished an umbilical plate (=umbilical coverplate here) and an internal septum from the chamber wall (Loeblich and Tappan, 1957). The umbilical coverplate and the internal septum were recognized as secondary structures which can be broken away in the final chamber. Reiss and Merling (1958) stressed that the toothplate (internal septum and umbilical plate of Loeblich and Tappan) is a primary formed structure, but they regarded the umbilical plate as chamber wall.

As to the toothplate of the Japanese *Pararotalia*, Ujiie (1966) described *P. nipponica* as follows: "tooth plate imper-

forate, extending from proximal margin of last intercameral foramen to distal (peripheral) margin of aperture, adhering its basal (umbilical) margin on proximal margin of spirothecal wall of last chamber throughout whole chamber-length, developing its upper (dorsal) free part broadly but very thinly in form of spatula with concave face turned to axial side and its upper anterior margin bent inwardly." Interestingly, the spatula-shaped portion of the upper toothplate has been interpreted as dissolved in the penultimate chamber based on a secondary wall which closes up an umbilical slit. His observation is similar to Loeblich and Tappan's umbilical plate formation model. However, a real image of the umbilical slit has not been clearly indicated. It may correspond to the interiomarginal slit of the aperture.

Hansen and Reiss (1971) indicated that the original wall structure of *Pararotalia* is identical to that of *Ammonia*. The umbilical coverplate (umbilical plate of Loeblich and Tappan, 1957) extends back from the foraminal plate to the preceding foraminal plate.

Hottinger *et al.* (1991) showed SEM micrographs of their defined toothplate of *P. inermis*. They describe the toothplate as "originating from the septal flap and connected to the inner ventral chamber wall, an imperforate toothplate extends to the distal chamber wall, attached to the dorsal corner of the primarily interiomarginal, extraumbilical aperture, and protruding with a free, serrated edge into the latter." Their toothplate is associated with a canal, which

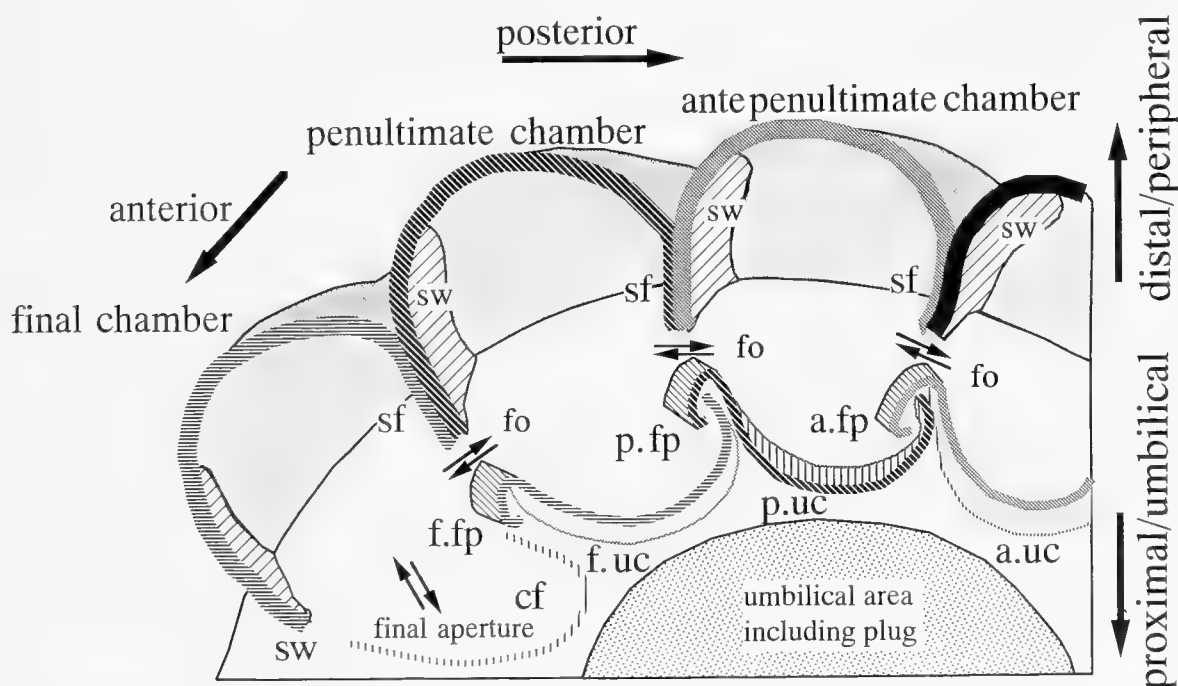


Figure 1. Schematic illustration of internal structure in the genus *Ammonia*. The aperture is an interiomarginal long slit extending from the peripheral side to the umbilicus. The final chamber continues to the foraminal plate and the umbilical coverplate of the penultimate chamber on the umbilical side. Thus, the coverplates around the umbilicus are delayed for one chamber lumen. The so-called toothplate corresponds to the ensemble of foraminal plate and umbilical coverplate. Abbreviations: a.fp=antepenultimate foraminal plate; a.uc=antepenultimate umbilical coverplate; cf=chamber flap; f.fp=final foraminal plate; f.uc=final umbilical coverplate; fo=foramen; p.fp=penultimate foraminal plate; p.uc=penultimate umbilical coverplate; sf=septal flap; sw=septal wall.

communicates with the chamber and with the furrow around an umbilical plug.

Descriptive terms for aperture and its related structure

In order to avoid confusion with respect to the aperture and foramen and their related structures, we use the following terms (Figure 1).

Chamber flap.—Original extension of chamber wall, covering umbilical sutural fissure, decorated with small spines.

Pararotalia forms an umbilical shoulder associated with nodes on this portion (Loeblich and Tappan, 1957), instead of forming a free chamber flap. [*chamber flap*: Cifelli, 1962] [*chamber lobe*: Parvati, 1971; Haynes and Whittaker, 1990] [*folium*: Hottinger *et al.*, 1991] [*lip*: Hofker, 1950, 1951a, b; Reiss and Merling, 1958; Seibold, 1971; Müller-Merz, 1980] [*umbilical lip*: Ujiie, 1965].

Foramen.—Opening connecting chamber lumina through septa, having a rounded, oval shape. Its shape is different from the final aperture. There are two types of foramen: the *Ammonia*-type and *Pararotalia*-type, based on the position and inclination of the foraminal plate to the walls of previous whorl (Figures 2, 3). [*intercameral foramen*: Smout, 1954] [*areal intercameral foramen*: Parvati, 1971] [*septal foramen*: Hofker, 1950, 1951a, b].

Foraminal plate.—Anterior plate extended from an umbilical coverplate (Figures 1, 2). It is formed on the proximal side of the aperture, leaving a foramen rounded or oval in shape. The foraminal plate is curled to the posterior out of the foramen, forming a hook-like structure in horizontal section (Figure 2), sometimes it is completely bent, resulting in

a columnar shape. This plate usually appears as an isolated plate adjoining the foramen of each chamber, including the final chamber, thereby some authors regarded it as a free structure of the toothplate. Our understanding of this plate agrees with the description of Hansen and Reiss (1971). They suggested that the chamber wall, septal flap, foraminal plate and umbilical coverplate are formed as one continuous structure. The foraminal plate of *Pararotalia* obliquely leans onto the chamber wall of the previous whorl and changes it to a protruded lip (lower lip) (Figure 3) [*anterior projection of umbilical plate*: Parvati, 1971] [*apertural lip*: Cifelli, 1962] [*foraminal plate*: Hansen and Reiss, 1971; Müller-Merz, 1980; Revets, 1993] [*internal septum*: Loeblich and Tappan, 1957] [*paries proximus*: Lévy *et al.*, 1986] [*toothplate*: Reiss and Merling, 1958; Ujiie, 1965, 1966] [*part of toothplate*: Hottinger *et al.*, 1991].

Hinge.—Junction of the foraminal plate and the umbilical coverplate. It delimits the proximal border or basal border of the foramen. In the *Ammonia*-type foramen, the hinge adheres to the umbilical/proximal side of the apertural opening on the previous whorl (Figure 2), and in the *Pararotalia*-type it adheres to the distal side of the aperture (Figure 3).

Labial aperture.—Opening usually formed on the posterior side of the chamber, except for the final one. Originally this foramen was denoted a protoforamen to distinguish it from a deutoforamen (Hofker, 1950, 1951a, b). Reiss and Merling (1958) recognized three parts of this aperture, namely, anterior, umbilical, and posterior. However, we recognized it as a single opening in the umbilical coverplate into the upper side of deeply incised sutures or sometimes into the umbilicus. The labial aperture is usually devoid of small spines around its opening. [*protoforamina*: Hofker,

Ammonia-type foramen

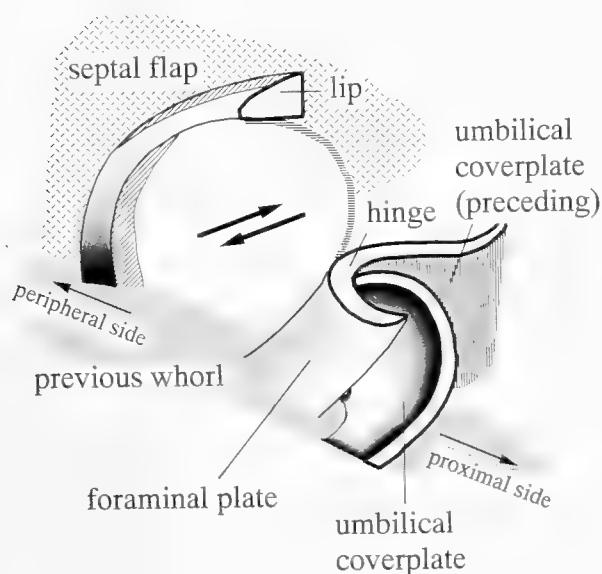


Figure 2. Schematic illustration of *Ammonia*-type foramen. The hinge, junction of the umbilical coverplate and the foraminal plate, butts against the previous whorl. The umbilical coverplate adheres to the preceding foraminal plate or the preceding umbilical coverplate.

Pararotalia-type foramen

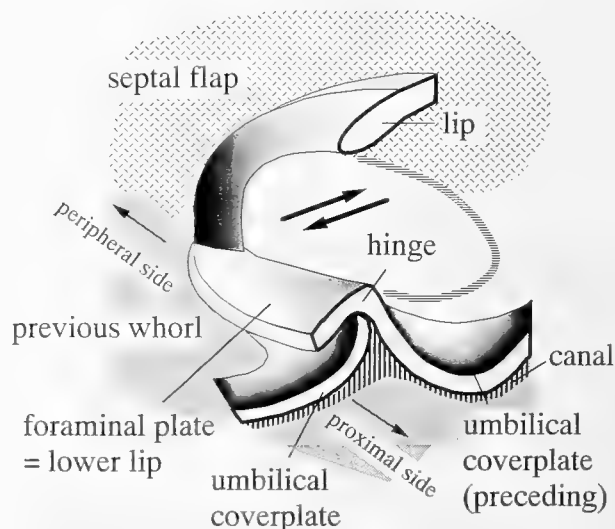


Figure 3. Schematic illustration of *Pararotalia*-type foramen. The hinge, junction of the umbilical coverplate and the foraminal plate, is much inclined toward the peripheral side of the aperture. Thus the foraminal plate appears as a protruded lip on the lower side.

1950, 1951a, b]

Lip.—Plate-like or tube-like structure formed in aperture and foramen. It is distinguished from the lower lip of *Pararotalia*. Sometimes the lip is referred to as the apertural rim.

Lower lip.—Lip usually associated with the foramen of *Pararotalia* and never seen in final aperture. It is formed by an adhesion of the basal part of the foraminal plate to the other, distal side of the final aperture, thereby the foramen of *Pararotalia* is areal. The lower lip is intrinsically the same as the foraminal plate, but structurally different. A tooth-

plate in the sense of Hottinger *et al.* (1991, 1993), which is a different concept from the so-called toothplate, corresponds to our lower lip. To avoid the confused usage of "toothplate," we do not use their toothplate.

Septal attachment.—Attachment of final septal wall to previous whorl, dividing the final aperture into two openings.

Umbilical coverplate.—Wall formed on the umbilical side of each chamber except for the final one, covered with chamber flap, usually forming a labial aperture in *A. japonica* and *A. tepida*, but usually without a labial aperture in *A. beccarii* and *P. nipponica*. This coverplate constitutes the

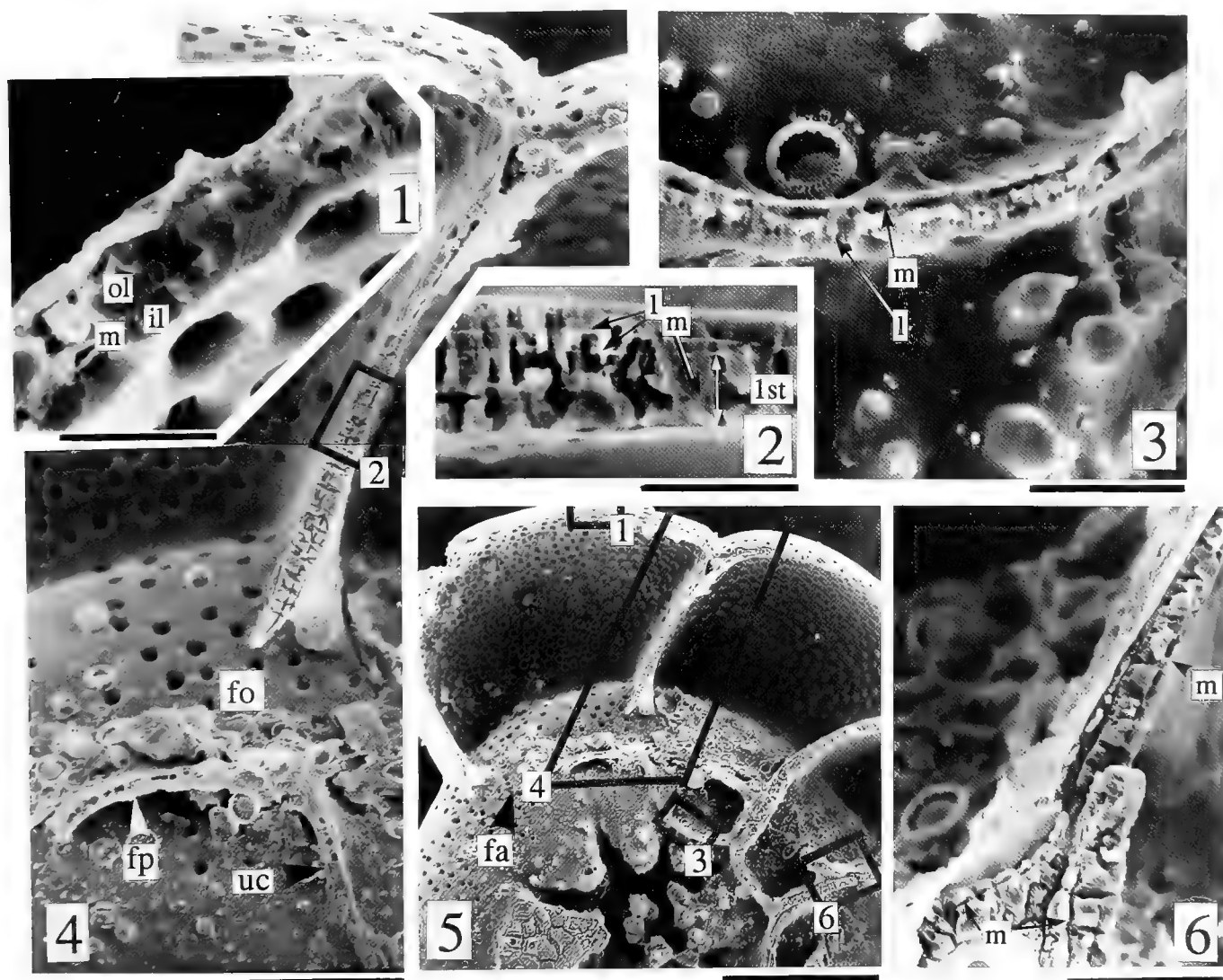


Figure 4. Walls of *Ammonia* sp. etched with 0.5 % phosphoric acid solution showing lamellar structures. **1.** Detail of the final chamber showing the outer layer (ol) and inner lining (il) divided by the incised median layer (m). Scale bar: 5 μ m. **2.** Detail of the penultimate septal wall (closeup of no. 4) showing the multiple layers (l) developed on the main bilamellar structure (1st) with the median layer (m). Scale bar: 5 μ m. **3.** Detail of the penultimate umbilical coverplate showing a trilamellar structure consisting of the primary bilamellar with median layer (m) and secondary layer (l) (closeup of no. 5). Scale bar: 5 μ m. **4.** Detail of the penultimate septal wall, the penultimate foramen (fo), the final foraminal plate (fp), and the final umbilical coverplate (uc). Scale bar: 23.1 μ m. **5.** Opened umbilical side of the final and the preceding chamber walls. fa=final aperture. Scale bar: 75 μ m. **6.** Detail of the junction of the ante-penultimate septal wall, the foraminal plate, and the umbilical cover plate (closeup of no. 5). m=median layer. Scale bar: 7 μ m

main part of the umbilical side of the chamber lumen and encloses the preceding foraminal plate. The foraminal plate should be an anterior projection of this coverplate. The foraminal plate lies within every chamber lumen, but the umbilical coverplate is located in the umbilical side of the preceding chamber. The umbilical coverplate is inclined to the previous whorl of the test, making a canal between the plate and the previous whorl in *Pararotalia*. [axial plate: Cifelli, 1962] [cover plate: Müller-Merz, 1980] [umbilical coverplate: Hansen and Reiss, 1971; Revets, 1993] [part of umbilical plate: Parvati, 1971] [retroparies: Lévy *et al.*, 1986] [umbilical plate: Loeblich and Tappan, 1957]

Lamellar structure

The final chamber wall of *Ammonia* sp. etched with phosphoric acid solution is typically bilamellar, consisting of inner and outer calcareous lamellae, and a middle incised lamella (in the sense of a primary organic membrane where calcification takes place; Hemleben *et al.*, 1977) (Figure 4.1, 4.5). Both the inner and outer calcareous lamellae extend back to cover the penultimate wall, but only the inner lining of the bilamellar structure is superimposed on the outer lamella of the penultimate septal wall, forming a septal flap (Smout, 1954). Such a lamellar structure has been illustrated by Hansen and Lykke-Andersen (1976). In addition to this model, we found multiple lamellae (originally bilamellar with an additional two calcareous lamellae) in the penultimate

septal wall near foramen (Figure 4.2, 4.4, 4.5), indicating that the preceding septal wall is not always three calcareous lamellae consisting of original bilamellar plus secondary lamella (= inner lining). This feature is not in agreement with the statements of Hansen and Lykke-Andersen (1976) and Hottinger *et al.* (1991), who noted a trilamellar structure for the preceding septal wall. Their demonstrations follow a typical model of layering. However, the secondary lamellae of the preceding septal walls are variable in different portions. Thus, it matters whether the section looked at was from the umbilicus or spiral side of the test. Our demonstration of multiple lamellae is based on a section from umbilical side of the test (Figure 4.5).

The final foraminal plate is very thin but clearly shows the bilamellar structure. The additional layering does not occur on the final and preceding foraminal plate, which keeps the wall in thin condition. The umbilical coverplate is originally bilamellar, connecting to the foraminal plate in the hinge, but this coverplate has additional layering. Figure 4.3 shows the trilamellar wall of the rudimentary umbilical coverplate consisting of the original bilamellar wall covered with a new secondary lamella. Although we morphologically defined the two apertural types in *Ammonia* and *Pararotalia*, the lamellar structure of the foraminal plate and umbilical coverplate of the *Pararotalia nipponica* is the same as observed in *Ammonia*.

The lamellar structure at the junction of the foraminal plate, umbilical coverplate and preceding septal wall is very

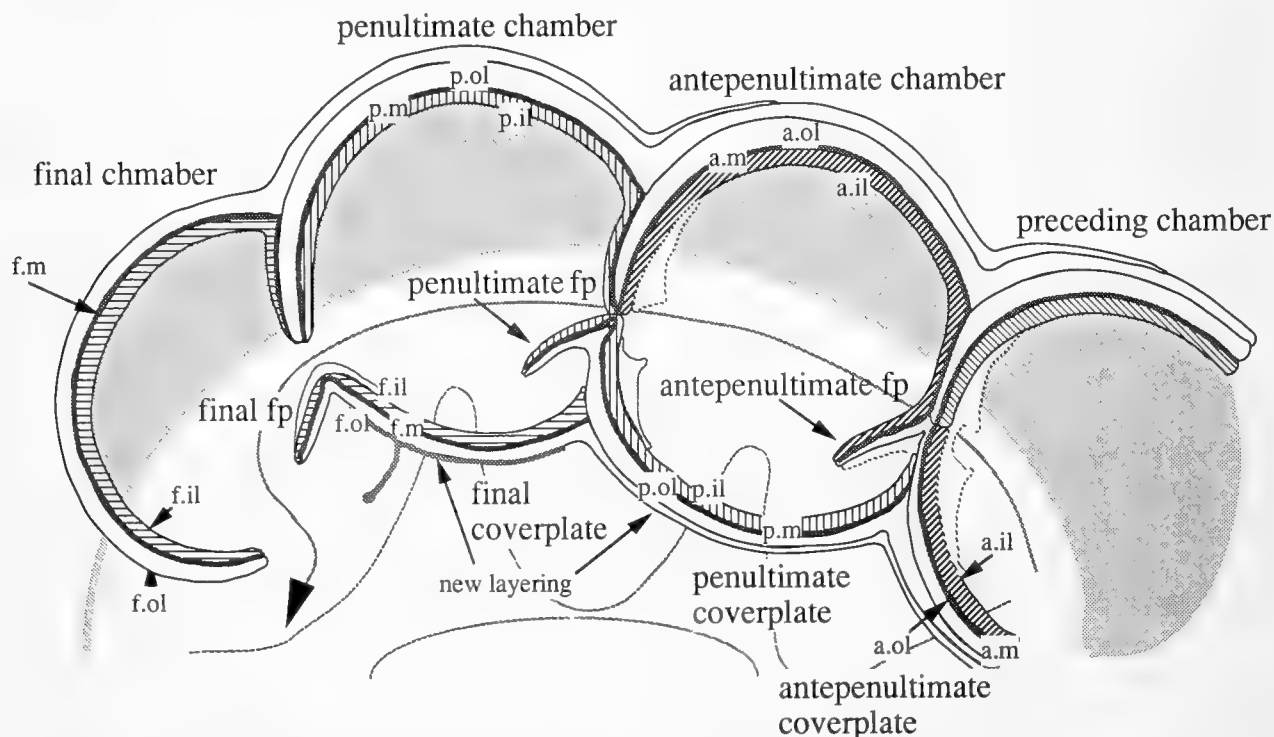


Figure 5. Schematically illustrated lamellar structure in the various parts of the last four chamber walls. Abbreviations: a.il=antepenultimate inner lining; a.m=antepenultimate median layer; a.ol=antepenultimate outer lamella; f.il=final inner lining; f.m=final median layer; f.ol=final outer lamella; p.il=penultimate inner lining; p.m=penultimate median layer; p.ol=penultimate outer lamella; fp=foraminal plate.

complicated (Figure 4.5, 4.6). The inner lining of the foraminal plate connects to the septal flap and the inner lining of the umbilical coverplate connects to the preceding inner lining of the septal wall. In Figure 5, the continuity and discontinuity of each lamella in various portions of the last four chambers are schematically illustrated. This lamellar model is similar to that of Hansen and Lykke-Andersen (1976), except for the median layer of the septal wall illustrated as a discontinuous layer at the junction area.

Description of apertural structures

Ammonia sp.

Figures 2, 4.1–4.6, 6.1–6.8, 7.1

Materials.—Over 10 specimens of *Ammonia* sp. from Recent sediment of brackish Lakes Shinjiko and Nakaumi, Japan. This form has been recognized as a major form of *Ammonia* in Japan, and is identical to *A. beccarii* forma A (Takayanagi, 1955, p. 44, text-figs. 31a–c, in part) and to *A. beccarii* forma 1 (Matoba, 1970).

Diagnosis of test.—The specimens are characterized by having nine to ten chambers in the final whorl, with an open umbilicus without a distinct plug, but with numerous spines in and around the umbilicus. Umbilical side of the test is flat or somewhat concave; spiral side is gently inflated. Periphery rounded, very slightly lobulate. Sutures are limbate and slightly inflated on the spiral side, but limbate and incised on the umbilical side. Imperforate chamber flap, associated with spines for each chamber, is developed and each flap is imbricated, covering the incised suture near the umbilicus. Chambers are transparent with numerous fine pores.

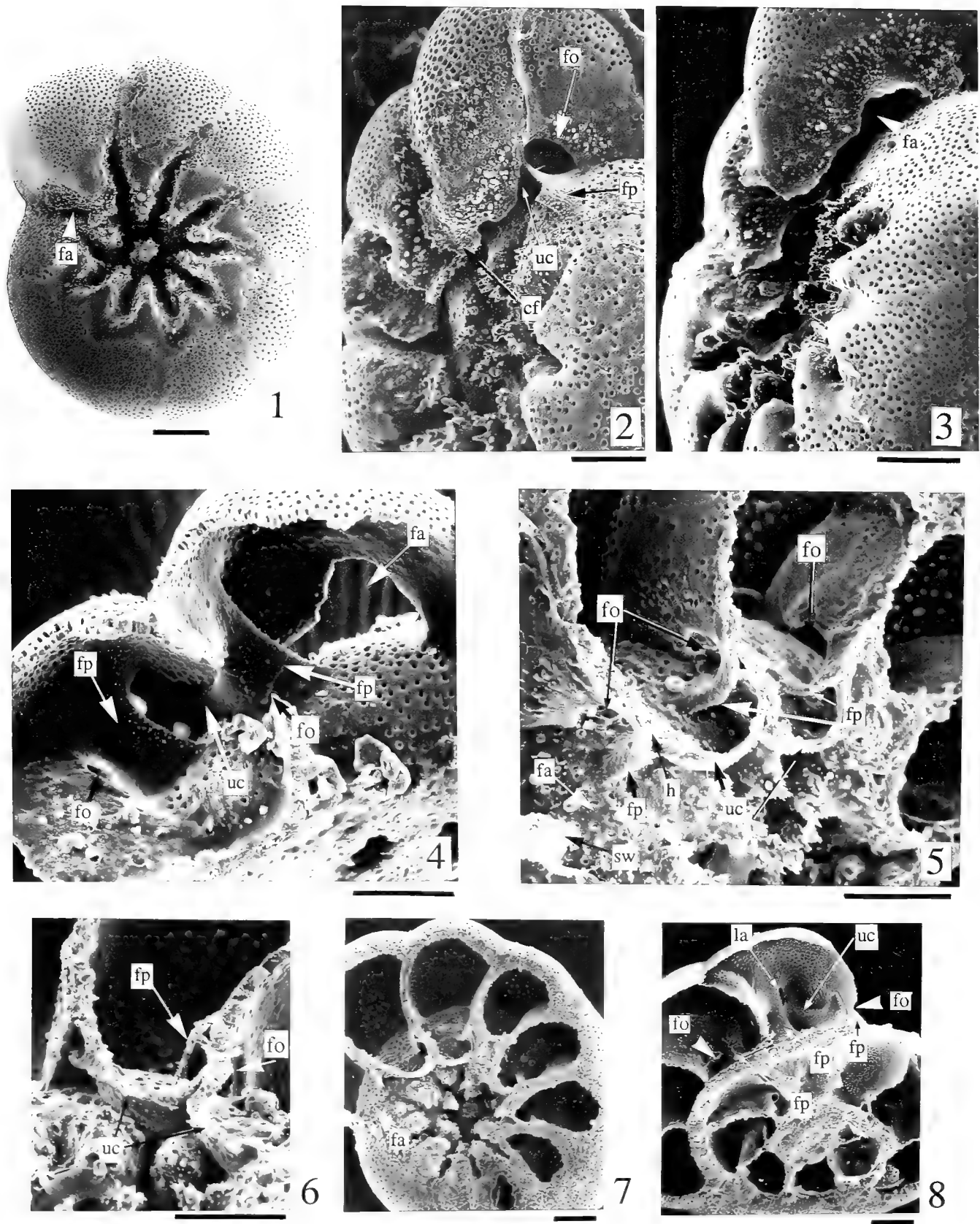
Apertural structures.—The final interiomarginal apertural opening is large without any free structure outside the aperture (Figure 6.1, 6.3). Thus the new foraminal plate is only formed between the foramen and proximal side of the finally formed chamber (Figure 6.2–6.4). When the new chamber is formed, the foraminal plate is usually covered with a new umbilical coverplate, which also covers the apertural opening (Figures 6.4–6.7, 7.1). Both the foraminal plate and umbilical coverplate are formed in a series of proximal side walls of the preceding chamber (Figure 6.5, 6.6). The foraminal plate is left, without further development in the chamber lumen, which shows a hook-like structure when observed in horizontal section (Figure 6.5). The umbilical coverplate is less perforate (Figure 6.4), sometimes forms a very small labial aperture (Figure 6.8). However, this is not significant for this species. Chamber flaps are decorated with small spines, imbricated around the depressed umbilical center, and they are not fused with each other (Figure 7.1). Sutures are always incised, having a fissure shape, but they do not form canals.

Remarks.—The examined species has been previously identified as *Ammonia beccarii* (Linné) by Japanese micropaleontologists. We doubt the taxonomic status of this species. *Ammonia beccarii* was originally collected from beach sands of the Adriatic Sea at Rimini, Italy. The type description given by Linné (1758) is not very helpful. In many subsequent works, *A. beccarii* has been broadly in-

terpreted as possessing wide variations in the test morphology. Cushman (1928) recognized three forms in *Ammonia beccarii*, which represent the different generations of this species. Thereafter Japanese micropaleontologists have used this taxonomic name for widely varied forms of *A. beccarii*. However, we cannot accept such forms in the Japanese *beccarii*. Typical *Ammonia beccarii* is characterized by a large test with well developed sutural knobs and fluted sutures on both dorsal and ventral sides. The number of chambers in the final whorl is about 13 chambers in *A. beccarii*, while the Japanese form has a smooth test surface without sutural knobs and usually less than 10 chambers in the final whorl. Thus the Japanese form is quite different from the typical form of *A. beccarii*. With respect to such morphological variation, Walton and Sloan (1990) recognized three different morphotypes in *Ammonia beccarii*. The Japanese form without the umbilical plug falls within the morphological range of their forma *tepida* and the form with the umbilical plug falls within the range of forma *parkinsoniana*. Schnitker (1974) based on the culturing of *Ammonia* and Walton and Sloan (1990) based on geographic distribution suggested a possible morphologic gradation between forma *tepida* and forma *parkinsoniana*, but no such clear gradation has been found between forma *beccarii* and the morphotypes *tepida* and *parkinsoniana*. Ecological observations show that *A. beccarii* (s.s.) and *A. tepida* have different morphofunctional adaptations to their habitats and environments (Debenay *et al.*, 1998). According to Debenay *et al.* (1998), *A. beccarii* (s.s.) lives on some algae as epiphytic life, whereas *A. tepida* lives in brackish sediments as endopelic life. The Japanese *A. beccarii* is similar to their *A. tepida*. Poag (1978) and Walton and Sloan (1990) mentioned that the geographic distribution of the typical form of *A. beccarii* (s.s.) appears to be limited to the Mediterranean, the eastern Atlantic coast and the western Atlantic coast from Florida to Nova Scotia. Whittaker (personal comm.) suggested that true *A. beccarii* lives only in the Mediterranean Sea and does not occur outside of it. These views are biogeographically supported, as no similarities exist between the Mediterranean fauna and the Indo-Pacific fauna (Rögl and Steiniger, 1984). Thus, no typical live or fossil *A. beccarii* occurs in and around Japan. This means the Japanese form does not represent *Ammonia beccarii* (s.s.).

Another problem in the systematics of *Ammonia beccarii* is introduced from DNA analysis. Pawlowski *et al.* (1995) showed a high similarity of the ribosomal DNA sequences between *A. beccarii* (s.s.) and the Japanese "*A. beccarii*." The Japanese form they examined in their DNA study is the same as we morphologically examined. Our morphologic comparison, however, indicates a taxonomic difference between the two entities. The different results arrived at by morphological comparison and molecular analysis cannot be reconciled at this time.

For these reasons, we hesitate to identify the Japanese form as *A. beccarii*, despite its being a well known species in brackish and shallow waters.



Ammonia japonica (Hada)

Figure 7.2–7.5

Type reference.—*Rotalia japonica* Hada, 1931, p. 137, text-figs. 93a–c.

Materials.—*A. japonica* (Hada) from Recent sediment of the Sakai Suido Strait near Miho Bay, the Sea of Japan.

Diagnosis of test.—Examined specimens are characterized by an inflated test with nine to ten chambers. Chambers are wedge-shaped toward the umbilicus. An umbilical plug is not usually developed in this species. The chamber flaps are less developed than in *Ammonia* sp. Radiate sutures on both the umbilical and spiral sides are straight. Umbilical sutures are incised and decorated with fine spines.

Apertural structures.—The final aperture is divided into two openings by the septal attachment (Figure 7.2–7.5). The anterior aperture is interiomarginal, with an arch-shaped opening and the posterior one is not easily seen, as it is covered by the chamber flap, but its shape is arched (Figure 7.4). The lip is somewhat protruded. The foraminal plates are curled and protrude out of the foramen when observed in horizontal section (Figure 7.3, 7.5). The foraminal plate without a free structure extends to form the ventral chamber wall in the final chamber (Figure 7.4). The umbilical coverplate is formed under the chamber flap when a new chamber is formed, but remains open in the upper part of the final aperture, forming a rounded labial aperture for each chamber but the final one (Figure 7.5). The chamber flap is triangular and points to the umbilicus and becomes larger as a new chamber is added, covering the labial aperture. Ventral sutures with small spines are deeply incised toward the umbilicus, like a fissure.

Remarks.—*Ammonia japonica* is morphologically distinguished from *Ammonia* sp. by having straight, radiate sutures on the dorsal side and a more inflated test. Development of the septal attachment is another characteristic feature of this species which distinguishes it from allied species. *Ammonia inflata* should be allied to *A. japonica* in having straight radiate sutures.

Ammonia sp.cf. ***A. parkinsoniana*** (d'Orbigny)

Figure 7.6–7.8

Type reference.—Cf. *Rosalina parkinsoniana* d'Orbigny, 1839, p. 99, pl. 4, figs. 25–27.

Materials.—Several specimens of *Ammonia* sp. cf. *parkinsoniana* from Recent sediment of brackish Lake Nakaumi.

Diagnosis of test.—Examined specimens are characterized by a thick lenticular test, having a distinct umbilical plug (Figure 7.6). The size is smaller than the examined form of *Ammonia* sp. The umbilical area is less decorated by spines and compact. The umbilical and spiral sides are inflated and the nonlobulate periphery is subacute. Chambers are eight to nine on the umbilical side and less inflated. Sutures on umbilical side are less incised and the ones on the spiral side are distinctly limbate for the test size. Walls are transparent with numerous fine pores and the test walls are brown in color.

Apertural structures.—The test morphology of *Ammonia* sp. cf. *A. parkinsoniana* differs from that of *Ammonia* sp. in having an umbilical plug and a small and more compact test. However, the apertural structure is very similar to that of *Ammonia* sp. (Figure 7.7, 7.8). The major difference is found in the less developed chamber flap (Figure 7.7). The final aperture is interiomarginal, mostly covered with a small chamber flap (Figure 7.7). The base of the foraminal plate adheres to the previous whorl and extends rearward to contact the umbilical coverplate. The umbilical coverplate covers the final apertural opening, leaving a rounded foramen (Figure 7.7). No labial aperture is formed in this species. Thus the foraminal plate is concealed by the umbilical coverplate, and remains in a plate-like structure in the preceding chamber lumen.

Remarks.—This form is identical to the form having the umbilical plug in *A. beccarii* forma 2 (Matoba, 1970, p. 48, pl. 5, figs. 11a–c, in part). Despite having the umbilical plug, this form is different from *Ammonia beccarii* (s.s.) on account of its small test and smooth test walls. According to Walton and Sloan (1990), this form falls within the range of morphotypic variation of *Ammonia beccarii* forma *parkinsoniana*. We tentatively identified this examined form with *Ammonia* sp. cf. *A. parkinsoniana*, pending further comparison with the type species.

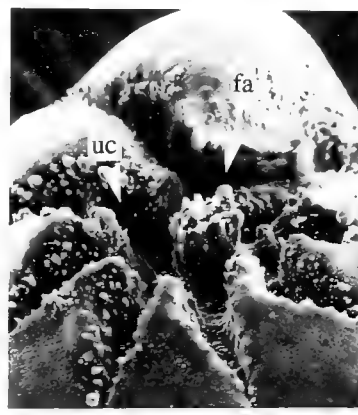
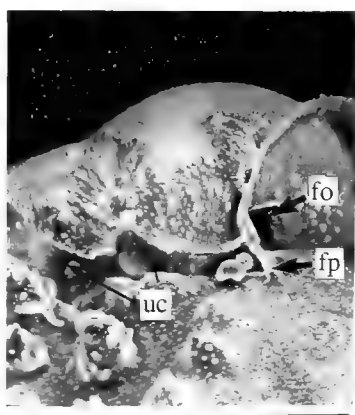
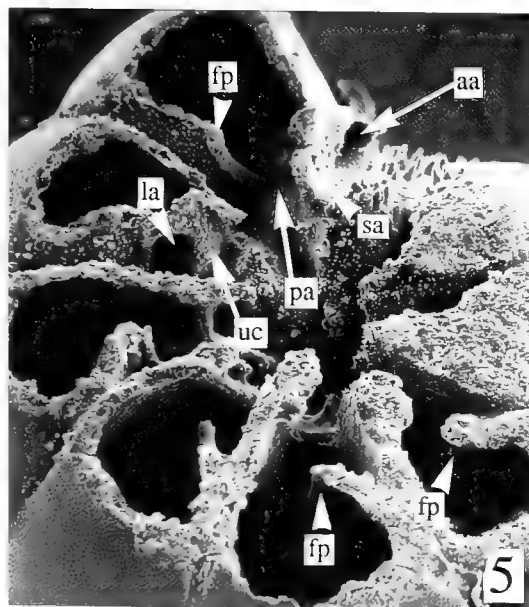
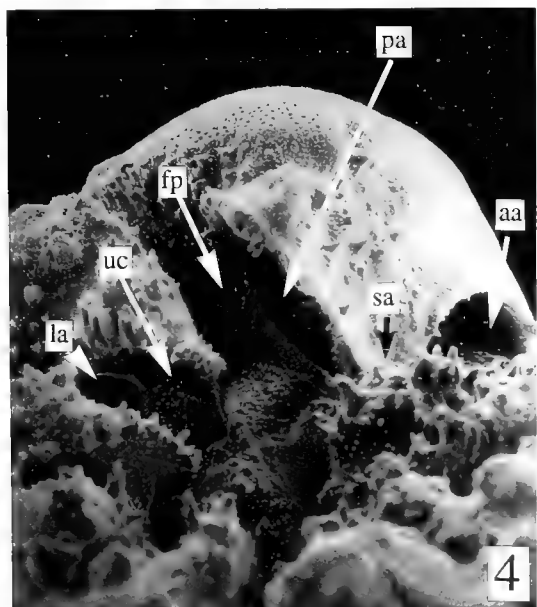
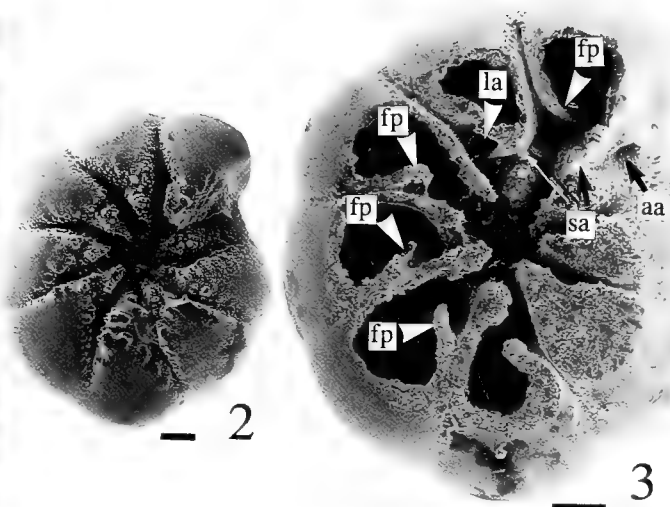
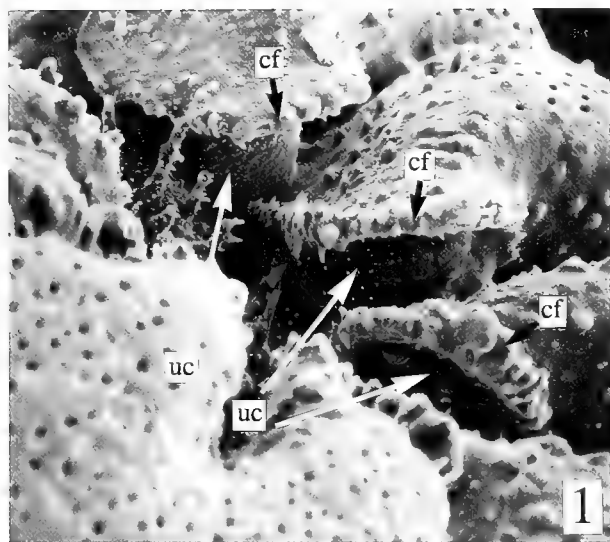
Ammonia tepida (Cushman)

Figure 8.1–8.3

Type reference.—*Rotalia beccarii* (Linné) var. *tepida* Cushman, 1931, p. 61, pl. 13, figs. 3a–c.

Materials.—*Ammonia tepida* (Cushman) from Recent sediment of the Sakai Suido Strait near Miho Bay, the Sea

Figure 6. External and internal apertural structure of *Ammonia* sp. Scale: 50 μ m. **1.** Umbilical side view. This form mostly has an open umbilicus. Fine umbilical plug is shown, but it is usually indistinct in optical observation. **2.** Oblique view of the umbilical side. The final chamber is removed, thus the penultimate foramen and the foraminal plate can be seen. The umbilical coverplates cannot be seen because they are concealed by the chamber flaps. **3.** Oblique view of the umbilical side. The final aperture is an interiomarginal slit from the peripheral side to the umbilicus. Note long slit of the apertural opening is different from rounded intercameral opening. **4.** Internal features of the final and penultimate chambers. Spiral side of walls is removed. Walls of the foraminal plate and the umbilical coverplate are smooth. **5.** Opened umbilical side showing the foraminal plates and the umbilical coverplates convex towards the umbilicus. The umbilical coverplate adheres to the hinge of the preceding foraminal plate and umbilical coverplate. **6.** The umbilical coverplate convex toward the umbilicus. The umbilical coverplate is curled and butts against the previous chamber whorl. **7.** External view of the opened umbilicus. **8.** Spiral side walls removed. Foraminal plate and umbilical coverplate shown in the penultimate chamber. Very small labial aperture may be seen in this specimen, but it is usually rare. Abbreviations: cf=chamber flap; fa=final aperture; fp=foraminal plate; h=hinge; fo=foramen; la=labial aperture; sw=septal wall; uc=umbilical coverplate.



of Japan.

Diagnosis of test.—This species has a small test for this genus and has six to seven chambers in the final whorl. The umbilicus is depressed, without a plug. Sutures incised and decorated with small spines on the umbilical side and flush with surface on the spiral side. Ventral chambers are broad and oval. Chamber flaps are developed, imbricated, and cover the sutures near the umbilicus.

Apertural structures.—The final aperture is interiomarginal and consists of a single opening extending to the umbilicus, with the developed chamber flap (Figure 8.1). The foraminal plate is formed on the proximal side of the foramen (Figure 8.2), and the hinge is much inclined and curled to connect to the posterior part of the chamber flap. Thus the posterior part of the chamber flap is concave where the labial aperture is formed except for the final chamber (Figure 8.1). The labial aperture is rather large and rounded in shape, which can be seen from a posterior oblique view (Figure 8.3). The umbilical coverplate is completely covered with the chamber flap, but always developed except in the final chamber (Figure 8.2).

Remarks.—Seibold (1971) put *A. tepida* in the genus *Discorbis*, based on differences of the internal structure such as the relationships between the toothplate (=foraminal plate), axial wall (=umbilical coverplate here), and septal lamellarity (that is, single or double). That idea is invalid, because these internal structures are not characteristic of *Discorbis*, but of *Ammonia*.

Lévy *et al.* (1986) pointed out no critical differences in the internal structure between *A. beccarii* and *A. tepida*. However, the development of the large labial aperture of *A. tepida* is not only significant in distinguishing this species from *A. beccarii*, but also from our examined *Ammonia* sp. herein. All examined specimens are in accordance with Cushman's original concept of *Ammonia beccarii* var. *tepida* (s.s.) and represent the typical *Ammonia beccarii* forma *tepida* of Walton and Sloan (1990). Although there are externally gradational morphologies in Walton and Sloan's forma *tepida*, our *tepida* is different from the other end member form (e. g., *Ammonia* sp. herein) in the presence of the labial aperture. *Ammonia tepida* may represent a definite species as suggested by Pawlowski *et al.* (1995). We are of the opinion that forma *tepida* of Walton and Sloan (1990) needs further consideration based on observations of the internal structure.

Ammonia tochigiensis (Uchio)

Figure 8.8, 8.9

Type reference.—*Rotalia tochigiensis* Uchio, 1951, p. 374, pl. 5, figs. 1a–c.

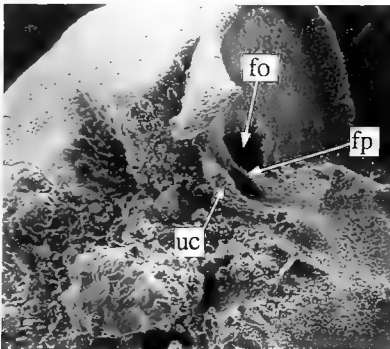
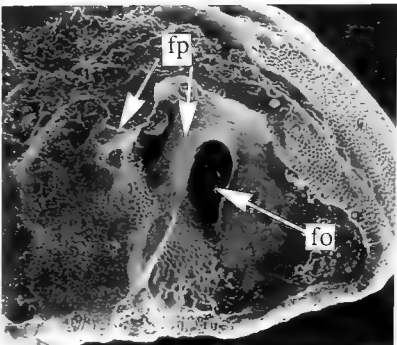
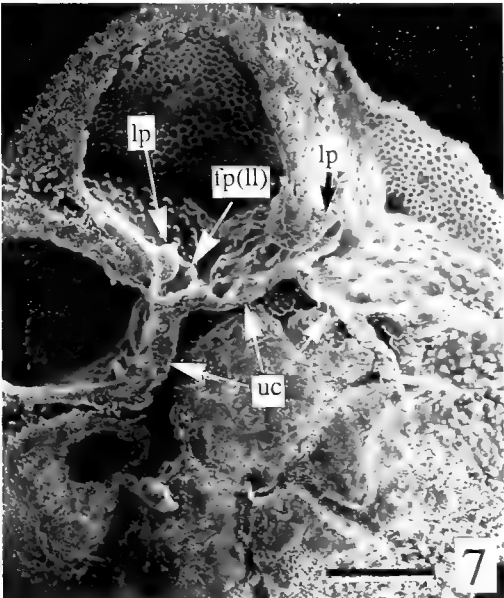
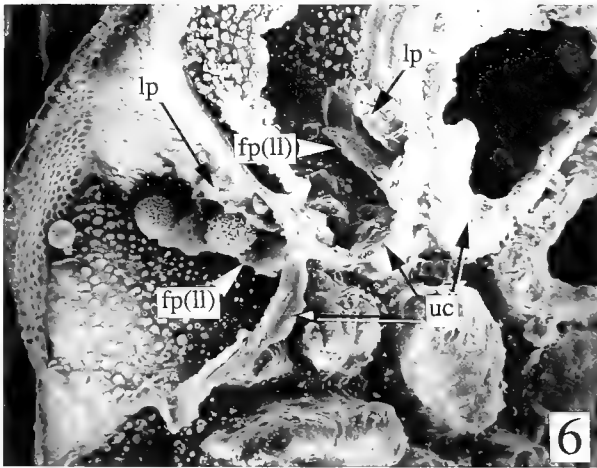
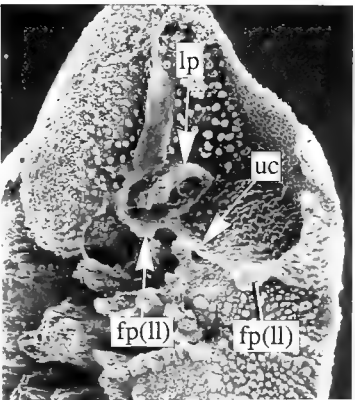
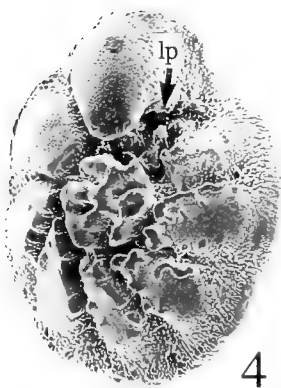
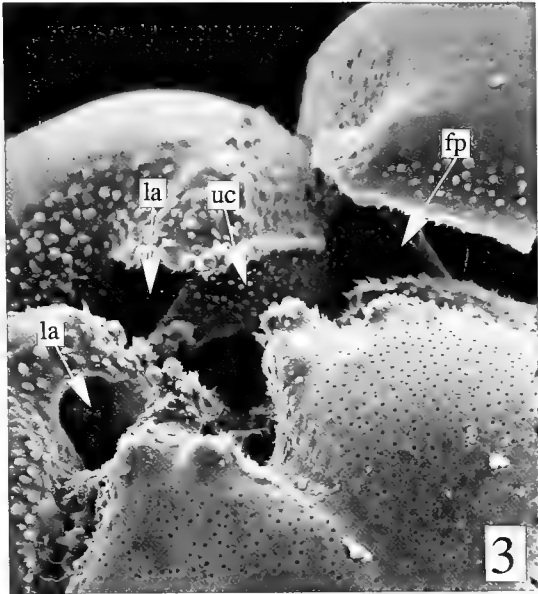
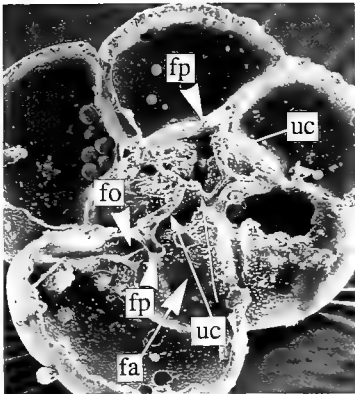
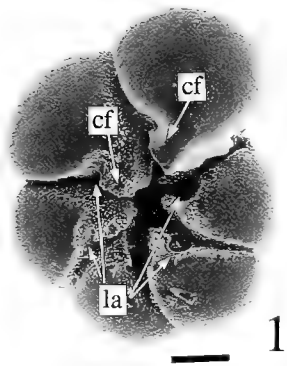
Materials.—One examined specimen from the type locality of this species, the Momiyama Formation, Tochigi Prefecture; five specimens from the Miocene Bihoku Group, Southwest Honshu, Japan. This species is very common in early middle Miocene shallow deposits of Japan.

Diagnosis of test.—Most examined specimens are naturally broken, without the final chamber, but well preserved specimens show the interiomarginal aperture. An umbilical plug is distinctly developed. Chamber flaps are less developed, thus chambers around the umbilical plug are serrated. 13–15 chambers in the final whorl. Sutures distinct and limbate on both sides of test and less incised on umbilical side. Sutures on spiral side are raised.

Apertural structures.—The final aperture is interiomarginal, mainly open on the umbilical side, but covered with a less developed chamber flap. The hinge is columnar in shape, formed at a high angle to the preceding whorl near the umbilicus, with a less developed free margin of the foraminal plate (Figure 8.8). The base of the foraminal plate on the previous whorl is strongly bent toward the posterior. The umbilical coverplate adheres to the edge of the preceding foraminal plate, leaving a concave space between the umbilical coverplate and the foraminal plate (Figure 8.9). Labial apertures are found in an incised suture near the umbilicus.

Remarks.—The internal structure with emphasis on the aperture has been discussed by Ujiie (1965). He described exactly the final aperture as showing an interiomarginal-basal narrow slit, but the description with respect to the foramen is unclear. We did not observe such a structure indicating "interiomarginal foramen converted from aperture, probably by partial resorption of apertural face slightly before addition of new chamber." His toothplate structure is not clearly distinguished from the chamber wall or the umbilical coverplate. His description says the free structure (foraminal plate?) is added after the formation of the new chamber. In our view the umbilical coverplate positioned in the penultimate chamber is formed simultaneously with the foraminal plate as well as the final chamber wall.

Figure 7. External and internal apertural structure of *Ammonia* sp., *Ammonia japonica* (Hada, 1931), and *Ammonia* sp. cf. *A. parkinsoniana* (d'Orbigny, 1836). Scale: 50 μ m. 1. Closeup figure of the chamber flaps and the umbilical coverplates in *Ammonia* sp. 2. Umbilical side view of *A. japonica*. 3. *A. japonica* with artificially removed chamber walls of the umbilical side. 4. Oblique view of the umbilical side of *A. japonica*. Proximal part of the septal wall adheres to the previous whorl in its final chamber (septal attachment in here), thus the anterior and posterior apertures are shown. The foraminal plate with its thickened rim represents the posterior end of the final chamber. 5. Oblique view of the umbilical side of dissected *A. japonica*. The posterior aperture changes into the labial aperture with development of the umbilical coverplate. 6. Umbilical side view of *A. sp. cf. A. parkinsoniana*. 7. Oblique view of the umbilical side of *A. sp. cf. A. parkinsoniana* without the final chamber. The umbilical coverplates seal the previous interiomarginal apertures. 8. Oblique view of the umbilical side of *A. sp. cf. A. parkinsoniana* showing opening of final aperture. No labial apertures are shown. Abbreviations: aa=anterior part of aperture; cf=chamber flap; fa=final aperture; fp=foraminal plate; fo=foramen; la=labial aperture; pa=posterior part of aperture; sa=septal attachment; uc=umbilical coverplate.



***Pararotalia nipponica* (Asano)**

Figures 3, 8.4–8.7

Type reference.—*Rotalia nipponica* Asano, 1936, p. 614, pl. 31, figs. 2a–c.

Materials.—*Pararotalia nipponica* (Asano) from Recent sediment of the Sakai Suido Strait near Miho Bay, the Sea of Japan.

Diagnosis of test.—The specimens examined are characterized by a well developed umbilical plug. Eight chambers on the umbilical side, inflated without a chamber flap, and having a rounded triangular shape around the umbilical plug. Sutures on the umbilical side are mostly radiate, deeply incised, but those on the spiral side are tangential. Umbilical spiral suture is covered with overhanging chambers (=umbilical shoulder), but it is never sealed up by the umbilical shoulders.

Apertural structures.—The final aperture is an interior-marginal slit, extending from the midbase of the apertural face to the umbilicus (Figure 8.4). The lip is thick and protruded. The chamber flap is undeveloped, thus the umbilical canal and sutural grooves are well shown as deep fissures on the umbilical side. The foraminal plate is only associated with the foramen and the base of its hinge adheres to the distal end of the preceding apertural opening, thereby forming the protruded lip (Figure 8.5–8.7), which is here called the lower lip (Figure 3). Thus the foramen is areal in position (Figure 8.5). The umbilical coverplate is developed around the umbilical plug except in the final chamber and connects to the foraminal plate (Figure 8.6, 8.7). No openings corresponding to a labial aperture are found in the umbilical coverplate, indicating the foramen is the main passage between the chambers.

Remarks.—The previously described toothplate of this species is morphologically very ambiguous and confused. The toothplate of Ujiie (1966) may correspond to the umbilical coverplate, according to his description and sketched figures (see above). He noted the umbilical slit (=aperture in original form) is closed with secondary calcification, and then the free toothplate disappears. Because of the absence of such a free structure in the penultimate and preceding chamber, he considered this to indicate partial dissolution of the toothplate. However, such an ingenious explanation is

unnecessary. Originally, there are no free structures comparable to his suggested structure in *P. nipponica*.

External test shape of *Pararotalia nipponica* is similar to that of *P. inermis*. We can observe the protruded structure demonstrated by Hottinger *et al.* (1991) on the umbilical side of *nipponica*'s foramen. This free part of the walls, which is called a toothplate by them, is structurally the same as the lower lip. We find also this type of foramen in *Neorotalia*, as can be seen in the detailed figures of Hottinger *et al.* (1991, 1993).

Discussion

Our observations suggest that the foraminal plate and umbilical coverplate complexes are variable at species level. Moreover, the interrelationships of these plates with neighboring structures are too complicated to easily understand without detailed anatomical observations. Thus, the simple application of the presence or absence of the so-called toothplate to taxonomic decisions is not a reliable criterion.

The foraminal plate and umbilical coverplate are a specified part of the chamber wall formed simultaneously in association with the preceding foramen. On this point, the final aperture is connected with the preceding foramen via the foraminal plate, which may be apparently correlated with the original toothplate concept of Hofker (1950, 1951a, b). Nevertheless, the critical point is that the foraminal plate involves both the final aperture and the preceding foramen. The umbilical coverplate serves only to seal the preceding apertural opening and is not associated with the formation of the final chamber wall. Such foraminal plate and umbilical coverplate structures are characteristic of the rotaliids, not of other taxa with a toothplate. The buliminid toothplate extends within the chamber lumen and no parts of it are concerned with the preceding chamber (e. g., Hofker, 1950, 1951a, b; Revets, 1989). We regard this difference of the toothplate as of primary importance in distinguishing the rotaliid aperture from others. Thus we follow the foraminal plate and umbilical coverplate concept of Hansen and Reiss (1971) and Revets (1993), who stressed the significance of applying only the terms foraminal plate and coverplate to rotaliid taxonomy rather than accepting the general toothplate concept.

Figures 8. External and internal apertural structure of *Ammonia tepida* (Cushman, 1931), *Ammonia tochiensis* (Uchio, 1951), and *Pararotalia nipponica* (Asano, 1936). Scale: 50 μ m. 1. Umbilical side view of *Ammonia tepida*. Note well developed chamber flaps. 2. Oblique view of the umbilical side of dissected *A. tepida*. The umbilical coverplates adhere to the preceding umbilical coverplate, apart from the hinge in this species. 3. Umbilical side view of *A. tepida* indicating the foraminal plate, umbilical coverplate, and labial aperture. 4. Umbilical side view of *P. nipponica*. The final aperture is an interior-marginal slit extending from the peripheral side to the umbilicus. 5. Oblique view of the umbilical side of dissected *P. nipponica*. The antepenultimate aperture is an oval surrounded by the lip and the lower lip (=foraminal plate). The remnant of the dissected penultimate chamber wall shows the lower lip linking to the umbilical coverplate. 6. *P. nipponica* with removed chamber walls of the umbilical side showing the lower lips and the umbilical coverplates. The lower lips represent the foraminal plates as a continuation to the umbilical coverplates. 7. Umbilical side view of *P. nipponica* with the final three chambers removed. The continuous structure of the lower lip (=foraminal plate) and the umbilical coverplate is clearly shown. The umbilical coverplates adhere to the previous whorl at a low angle. 8. Peripheral view of dissected *A. tochiensis*. Columnar-shaped foraminal plate is due to a posterior bend of the plate. The umbilical coverplate adheres to the bent edge of the preceding plate. 9. Oblique view of the umbilical side of dissected *A. tochiensis*. The complex of foramen, foraminal plate and umbilical coverplate is shown in the antepenultimate chamber. Abbreviations: cf=chamber flap; fa=final aperture; fp (ll)=foraminal plate (lower lip); fp=foraminal plate; fo=foramen; la=labial aperture; uc=umbilical coverplate; l=lip.

On the other hand, different opinions appeared in the discussion and description of the rotaliids by Hottinger *et al.* (1991, 1993). They are consistent in using the term toothplate by revising its concept. In addition to the original concept, their toothplate includes a new point of view such as an association with a canal. They defined the toothplate as "A toothplate separates partly or entirely the main chamber lumen from an axial space....Interconnected toothplates produce a primary canal." According to their definition, *Pararotalia* is associated with a toothplate as it has an umbilical canal, while *Ammonia* is not associated with a toothplate as it has no umbilical canal. The presence or absence of their toothplate is due to whether the canal is formed or not. Their toothplate concept in relation to structures such as foraminal plate, umbilical coverplate and umbilical plate is subordinate in significance. As we observed in the aperture of *Pararotalia*, the umbilical coverplate obliquely leans to the walls of the previous whorl. The inclination of the foraminal plate is much the same as the umbilical coverplate and changes to a lip in this type of foramen (Figure 3). Thus we usually observe the canal between the umbilical plate/foraminal plate and the previous whorl of the test. This structural reconstruction is similar to that of *Neorotalia* demonstrated by Hottinger *et al.* (1991, p. 29, figure 7) and *Pararotalia* (Hottinger *et al.*, 1993, p. 141, pl. 200, figs. 10, 11). This means that their toothplate is nothing but our foraminal plate, which is here called the lower lip in order to emphasize the structural difference from the *Ammonia*-type foramen. The same view can be seen in Revets (1993), who stated "The internal structures delimiting the canals are the perfect homologues of the foraminal- and coverplate of *Ammonia*."

In addition to different interpretations for the toothplate among these authors, there are also discrepancies with respect to the lamellar structure. Hansen and Reiss (1971) observed that the foraminal plate is bilamellar. Later, Revets (1993) confirmed the bilamellar structure of the rotaliid genus *Neorotalia*, along with the taxonomic significance of the buliminid toothplate consisting only of a modification of the inner lining. Hottinger *et al.* (1991) state that the septal flap, consisting of the inner lamella (=inner lining), may extend into the foraminal plate, coverplate, and toothplate. Thus an additional inner lamella is imposed on the original bilamellar walls, producing trilamellar walls. A similar view of lamellar structure was suggested by Revets (1993) when he stated "As the coverplate butts into the foraminal plate of the prepenultimate chamber, it covers its outside by a secondary lamella, so that this foraminal plate cum coverplate is trilamellar." Our observations of *Ammonia* sp. indicate, however, that the foraminal plate is always bilamellar and the preceding umbilical coverplate is covered with an outer lamella of newly formed coverplate (Figure 5). The foraminal plates never receive additional lamella from the new umbilical coverplate. We need further comparisons to ascertain the variation in the lamellar structure.

Conclusions

We studied the internal structure of some Japanese species of the genera *Ammonia* and *Pararotalia* to validate

Hofker's original concept of the toothplate (Hofker, 1950; 1951a, b). Two major structures, the foraminal plate and the umbilical coverplate (Hansen and Reiss, 1971), are distinguished instead of the general term toothplate. The lamellar structure of the foraminal plate and umbilical coverplate is originally bilamellar. Two types of aperture except for the final one, *Ammonia*-type and *Pararotalia*-type foramen, are recognized, according to the position of the foraminal plate constructed in the aperture. The description of the foraminal plate/umbilical coverplate structure is significant to rotaliid taxonomy in understanding intraspecific morphological variation. However, the structural complex should not be treated as a unit in order to make generic-level distinctions.

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The turrilitid ammonoid *Mariella* from Hokkaido—Part 3 (Studies of the Cretaceous ammonites from Hokkaido and Sakhalin—LXXXVII)

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Abstract. *Mariella (Mariella) lewesiensis* (Spath, 1926) from the Cretaceous of the Hobetsu district, south-central Hokkaido, is described. It is represented by a large specimen, from which a question may arise about the previous view of dimorphism. This species is not directly related to *M. (M.) dorsetensis* (Spath, 1926). It has some affinities with *M. (M.) cenomanensis* (Schlüter, 1876).

Key words: Cretaceous, dimorphism, Hokkaido, *Mariella (Mariella) lewesiensis*, Turrilitidae

Introduction

Altogether eight species of the genus *Mariella* from Hokkaido have been described successively in Part 1 (Matsumoto *et al.*, 1999) and Part 2 (Matsumoto and Kawashita, 1999) under the same title as this paper. They are based primarily on a number of specimens from the mid-Cretaceous members of the Middle Yezo Subgroup in the Soeushinai area [=Shumarinai–Soeushinai area by some authors] of northwestern Hokkaido and on supplementary material from the correlative part in the Yubari Mountains of central Hokkaido.

An additional species of *Mariella* described here is represented by a large specimen which was found by T. K. from the Hobetsu district of south-central Hokkaido. At the request of the Mikasa City Museum [MCM] the specimen was temporarily put on public display there without, however, its being assigned specific name. With the consent of MCM we have recently investigated it to settle its systematic allocation. The described specimen is now officially registered at the National Science Museum [NSM] in Tokyo as a donation by T. K.

Paleontological description (continued)

Mariella (Mariella) lewesiensis (Spath, 1926)

Figures 2–4

Turrilites bergeri Sharpe, 1857, p. 65 (*pars*), pl. 26, fig. 10 only.

Turrilites lewesiensis Spath, 1926, p. 429.

Mariella lewesiensis (Spath). Spath, 1937, p. 512.

Mariella (Mariella) dorsetensis (Spath, 1926). Renz *in*, Renz *et al.*, 1963, p. 1095, pl. 1, fig. 3; Klinger and Kennedy, 1978, p. 31, pl. 9, fig. F, text-figs. 3A, 8A; Kennedy *et al.*, 1979, p. 18, pl. 1, fig.

9.

Mariella (Mariella) lewesiensis (Spath, 1926). Kennedy, 1971, p. 27, pl. 8, figs. 1, 4, 5, 8; Juignet and Kennedy, 1976, p. 62, pl. 3, fig. 17; Atabekian, 1985, p. 37, pl. 7, fig. 1; pl. 8, fig. 1; Wright and Kennedy, 1996, p. 339, pl. 100, figs. 4, 13, 23, 27; pl. 101, figs. 2, 3; pl. 103, figs. 6–8.

Type.—Holotype, by monotypy, is BMNH 3355B, the original of Sharpe, 1857, pl. 26, fig. 10 (reillustrated by Wright and Kennedy, 1996, pl. 101, fig. 3). It was studied by T. M. at the British Natural History Museum (BMNH) in 1979.

Material.—NSM PM16123. This specimen was collected by T. K. on 19 September 1973 at his locality no. 21 from the mudstone outcrop on the right side of a stream called the Matsukashimapu, about 600m NW of Sanushi Bridge, Inasato area in the Hobetsu district, south-central Hokkaido (Figure 1). The geologic structure is complicated in the Inasato area, where strata seem to be much disordered by folding and thrusting.

Description.—The specimen (Figures 2, 3) is in the state of half-ammonoid preservation (see Maeda, 1987 for this technical term). It is, however, magnificent in its large size, nearly 270mm in total height consisting of 7 preserved whorls and roughly 120mm in diameter at the last whorl (i.e., part of the body chamber). It would be nearly 400mm in tower height, if the missing younger whorls were added. The estimated apical angle is 21°. The late part (at the fifth whorl from the preserved top in Figure 2) is secondarily displaced from the main part, whereas the middle whorl (the third whorl from the preserved top) is almost undeformed.

The septal suture is partly exposed on this whorl (Figure 4).

The upper part of the exposed whorl face is broadly convex and smooth. It slopes down to the gently convex or nearly vertical main flank, which in turn slopes down

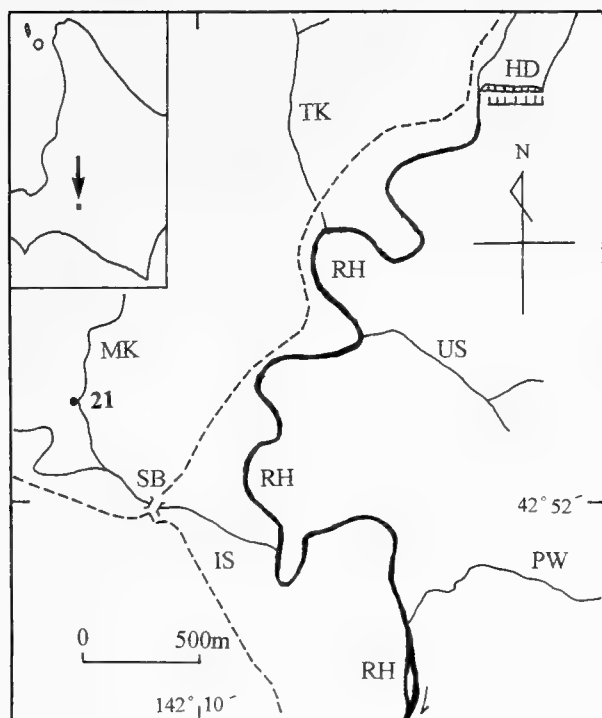


Figure 1. Map showing the location of T. Kijima's Loc. 21 where *Mariella (Mariella) lewesiensis* (Hobetsu specimen) was obtained. HD=Hobetsu Dam; IS=Inasato; MK=Matsukashimapu-zawa; PW=Penke-wakka-tannenai-zawa; RH=River Hobetsu; SB=Sanushi Bridge across the River Sanushibe; TK=Takikawa-no-sawa; US=Uesugi-zawa. The term sawa or zawa means a rivulet. Broken line: highway.

considerably inward. Thus the interwhorl junction is deeply impressed.

Each whorl is ornamented by tubercles in four rows. The tubercles of the upper two rows are coarse and fairly strong, although those of the second row are slightly smaller than those of the first row. On the whorls of the early to middle growth stages the tubercles are somewhat transversely and obliquely elongated. In later growth stages the tubercles of the upper two rows are very coarse, showing a subelliptical base, a domelike shape and a spinose peak. The tubercles of the third row are somewhat smaller than those of the second row in the early to middle growth stages. In the later growth stages they become much smaller, weaker and obliquely clavate (i.e., spirally elongated) in contrast to the enlarged tubercles of the upper two rows. The three rows on the exposed whorl face are disposed at subequal but slightly decreasing intervals downward (Figures 2, 3).

The tubercles of the fourth row are close to those of the third and run along the lower whorl seam, giving crenulation to the interwhorl junction. They are scarcely visible in earlier growth stages, but become more obvious on the lower whorl face in later stages. The tubercles of the first to fourth rows are aligned in an obliquely adoral orientation, but they do not form clear ribbing. Although the basal surface is not fully exposed, distinct ribs do not seem to run from the tuber-

cles of the fourth row. A series of shallow dimplelike depressions is discernible between the upper two rows of tubercles, but it does not form a wide and deep furrow like that of *Mariella (Wintonia)*.

Comparison.—The middle part of this specimen is comparable with the septate holotype and some other example of *M. (M.) lewesiensis* (e.g., Wright and Kennedy, 1996, pl. 101, figs. 3, 2; Atabekian, 1985, pl. 8, fig. 1). In its less deformed whorl, i.e., the third whorl from the top, the height [H] is 32mm at diameter [D] 72mm, hence, H/D is 0.47. These proportions conform with those of the holotype at a corresponding stage, where H=30.5mm, D=67.0mm and H/D=0.47. Similarity is also observable in the ornament. There are 21 tubercles in each row per whorl in the holotype. The Hobetsu specimen shows eleven tubercles in the exposed half of the whorl at the middle growth stage, although the number seems to decrease to 7 or 8 at the last stage. The smooth surface in the upper part of the exposed whorl face immediately below the upper seam is a diagnostic character of this species. This feature is clearly observed in the Hobetsu specimen. The faint ribbing on the basal surface in this species also occurs in our specimen. To sum up, the described specimen is certainly identified with *M. (M.) lewesiensis*.

Discussion.—The Hobetsu specimen attains enormous size for *Mariella (M.) lewesiensis*. This raises the problem of dimorphism. Wright and Kennedy (1996, p. 340) have pointed out a dimorphic pair in this species, namely they regarded SMC B35910 (Wright and Kennedy, 1996, pl. 103, fig. 7) as an adult macroconch and SMC B35905 (Wright and Kennedy, 1996, pl. 100, fig. 27) as an adult microconch. The former is about 200mm in estimated original tower height with an inferred apical angle of 22°, whereas the latter is about 150mm in tower height with an apical angle of 21°.

The specimen from Hobetsu is almost twice as large as the so-called macroconch example (SMC B35910) from England in regard to the total whorl height (400mm) and also to the diameter (120mm) of the last whorl. This fact throws doubt on the previous evidence of dimorphism in *M. (M.) lewesiensis*. Further investigation, including the statistical examination on a sufficient number of specimens, is required for a definite conclusion.

Mariella (M.) lewesiensis has been often confused with *M. (M.) dorsetensis* (Spath). This is shown by the synonymy given in the description of the latter in Part 1 (Matsumoto *et al.*, 1999, p. 107) and that of the former in Part 3. Here we would like to comment that the two specimens illustrated by Benavides-Cáceres (1956, p. 108, pl. 40, figs. 8, 9) under "*Paraturrilites lewesiensis* (Spath)" should both be revised to *M. (M.) dorsetensis* (Spath), although one of them (Benavides-Cáceres, 1956, pl. 40, fig. 8 only) was considered so by many authors. Likewise, what was called *M. (M.) lewesiensis* (Spath) by Marciniowski (1974, pl. 32, fig. 13 without description), from the Lower Cenomanian of the Polish Jura Chain, is probably *M. (M.) dorsetensis*, because of the distinct ribs on the upper whorl face and the rows of granular tubercles on the convex flank at subequal intervals.

The morphological distinction between the two species has been already discussed in Part 1 (Matsumoto *et al.*, 1999). We offer here remarks on their affinities. *M. (M.)*



Figure 2. *Mariella (Mariella) lewesiensis* (Spath). Lateral view of NSM PM16123, $\times 2/3$. (Photo courtesy of Katsumi Shinohara, without whitening)



Figure 3. *Mariella (Mariella) lewesiensis* (Spath). NSM PM16123. Specimen turned about 60° clockwise from the position in Figure 2, $\times 2/3$. (Photo courtesy of Katsumi Shinohara, without whitening)



Figure 4. *Mariella (Mariella) lewesiensis* (Spath). External suture partly exposed on the preserved third whorl of NSM PM16123. E: external lobe; L: lateral lobe. Bar scale: 5 mm.

dorsetensis is closely allied to *M. (M.) bergeri* (Brongniart) of latest Albian age. The affinities of *M. (M.) lewesiensis* have not been much discussed, but recently Wright and Kennedy (1996, p. 344) have pointed out a close relationship between *M. (M.) lewesiensis* and *M. (M.) cenomanensis* (Schlüter, 1867). We would agree with them, although well preserved examples of *M. (M.) cenomanensis* have not been described from Hokkaido. Based on the description and plentiful illustrations by Wright and Kennedy (1996, p. 342, with a full synonymy, and pl. 100, figs. 3, 24, 26; pl. 101, figs. 1, 4; pl. 102, fig. 14; pl. 103, fig. 9; pl. 110, fig. 3; pl. 111, figs. 1, 3; text-figs. 136A and 141B; also Wright and Kennedy, 1995, text-fig. 129E for the suture), the following points are evident. In *M. (M.) cenomanensis* the upper part of the exposed whorl face is convex and smooth as in *M. (M.) lewesiensis*. The tubercles of the upper two rows are coarse in both species, but in the former the tubercles of the second row are clavate (i.e., spirally elongated) and disposed in the lower part of the flank, being separated from the first row by a broad, smooth zone. Some examples of *M. (M.) cenomanensis* (e.g., Wright and Kennedy, 1996, pl. 101, figs. 1, 2) are nearly as large as the Hobetsu specimen of *M. (M.) lewesiensis*.

Incidentally, "*Mariella (Mariella)* n. sp. aff. *lewesiensis* (Spath)," was mentioned by Kanie *et al.* (1977, p. 113, pl. 1, fig. 8) in their Madagascar paper. Actually it is one of the specimens (TKD 30080A from Loc. 71204 in the Shumarinai area) of *M. (M.) dorsetensis*, as has been recently described by Matsumoto *et al.* (1999, p. 108).

Distribution.—*Mariella (M.) lewesiensis* has been reported to occur in the Lower Cenomanian of southern England, France, Germany, Switzerland, Poland, Turkmenistan, Iran, Zululand (South Africa) and Madagascar (see synonymy for the references). Now its distribution is extended to Japan in the northwestern Pacific region.

Acknowledgments

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Dicotyledonous leaf macrofossils from the latest Albian-earliest Cenomanian of the Eromanga Basin, Queensland, Australia.

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Abstract. Ten types of dicotyledonous angiosperm cuticle are described from bore core samples from the Early Cretaceous (latest Albian-earliest Cenomanian) of the Eromanga Basin, central Queensland. To date, these are the oldest organically preserved angiosperm macrofossils in Australia. Most of this material is found as small dispersed fragments, but two more intact lobed leaves were found. The affinities of some specimens are suggested to lie with the Chloranthaceae and Illiciaceae, and possibly the Platanaceae, but the rest are unknown. None of the cuticles show the paracytic stomatal arrangement which is common in extant plant families often regarded as 'primitive'. However, one of the cuticle forms exhibits a 'plastic,' variable form of subsidiary cell arrangement, which has previously been suggested as the most primitive condition. These angiosperms were a small component of an overwhelmingly gymnosperm (mostly conifer) dominated flora. They grew in clastic swamps, but may also have occurred in coal swamps or sandy levees. The notably thin cuticle of some forms is consistent with an understory or deciduous habit.

Key words: angiosperm, Australia, Cretaceous, cuticle, stomate

Introduction

The first angiosperms appeared in Australia during the Barremian-early Aptian, and by the end of the Albian over 20 angiosperm(id) pollen types are known (Burger, 1990). Based on pollen records the angiosperms had originated somewhere distal to Australia by the Valanginian (Brenner and Bickoff, 1992; Brenner, 1996). The oldest angiosperm macrofossils in Australia are impressions from the Aptian of the Otway Basin in Victoria (Douglas, 1994). These impressions include a dicot identified as *Hydrocotylophyllum lusitanicum* Teixeira (Douglas, 1965). A further specimen, previously interpreted by Drinnan and Chambers (1986) as a possible fern, was later claimed as the world's oldest flower (Taylor and Hickey, 1990; although this distinction is now claimed by Late Jurassic material from China, Sun *et al.* 1998). The Australian Late Cretaceous angiosperm macrofossil record is very poor, probably due to a lack of outcrop. Scattered impressions and some cuticular debris are known from drill core material from the later part of the Victorian Cretaceous but have not been formally documented. McLoughlin *et al.* (1995) illustrated several dicotyledonous leaf impressions of probable Cenomanian age from the Eromanga Basin of central Queensland. Their material came from surface outcrop of the Winton Formation (Vine and Day, 1965; Exon and Senior, 1976) which has

undergone considerable weathering. Below this zone, in samples obtained from bore cores for this study, weathering and lithification have been minimal and anatomical details (including cuticle) of fossil plants are preserved (Pole, 1999; Pole and Douglas, 1999). This material has been dated palynologically as close to the Albian-Cenomanian boundary (Dettmann and Playford, 1969; Helby *et al.*, 1987; Dettmann *et al.*, 1992). The purpose of this paper is to document the dicotyledonous macrofossils from bore core samples of the Eromanga Basin.

Dicotyledon leaf fragments were recognised by having net venation comprising more than one order, or thickness of veins, and confirmed with epidermal characters. Angiosperm cuticle was recognised partly by its robustness, i. e. it is strong enough to survive processing and handling. This eliminates from consideration the ferns, which in any case, are generally distinct on morphological characters (van Cotthem, 1970a). The Early Cretaceous fern *Weichselia*, which does have relatively thick cuticle, is singularly unique in morphology. *Weichselia* is more similar to *Equisetum* and some gymnosperms (Alvin, 1974), having relatively large, randomly oriented guard cells, which are not sunken or over arched by subsidiary cells, but have an outer stomatal ledge. On these criteria there is little else in the Early Cretaceous which could be confused as dicotyledonous, with the possible exception of the Caytoniales. Harris

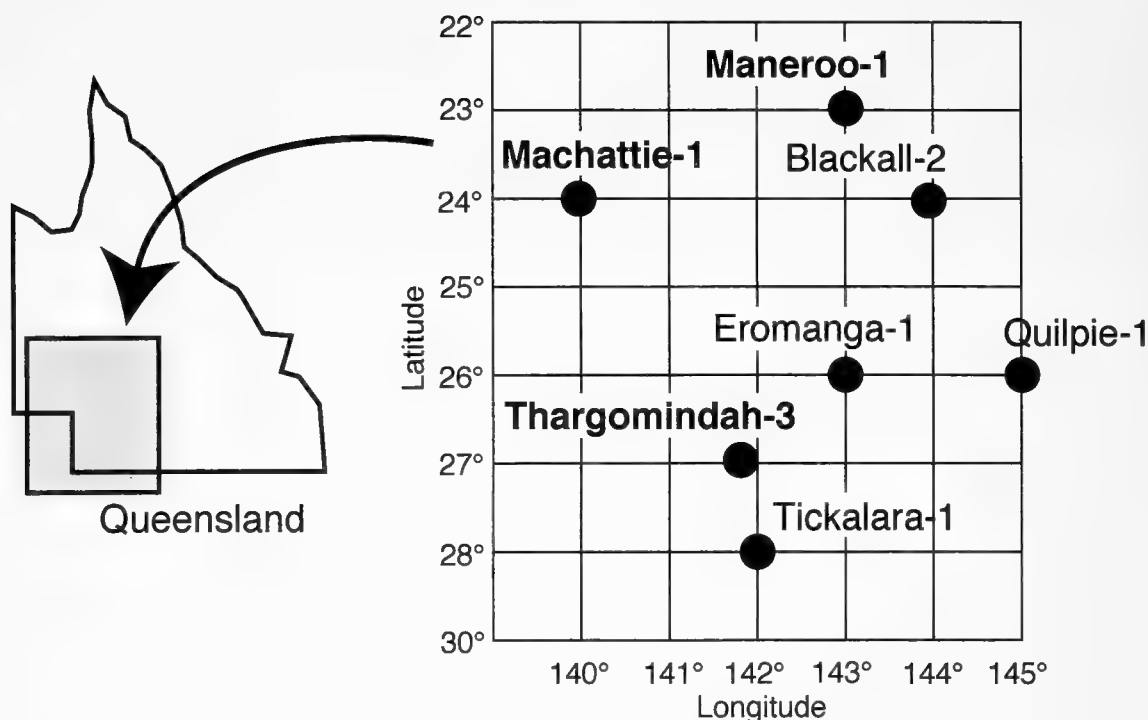


Figure 1. Locality map. The position of the study area within Queensland, Australia, is shown at left, and the position of all drill cores sampled within the study area is shown at right. Names of drill cores which provided dicotyledonous cuticle are in bold.

(1940) described *Sagenopteris* cuticle which had guard cells, apparently (according to his sketch) without outer stomatal ledges, no distinct subsidiary cells, and trichomes with basal cells. A cuticle type from the Winton Formation with possible affinities to the Caytoniales is described in Pole and Douglas (1999). Monocotyledon cuticle is generally distinct and is discussed in Pole (1999).

My separation of fossil cuticles into morphological groups is based on my experience with the cuticle of extant plants. In my opinion the forms described below represent individual species.

Materials and methods

Seven bore cores were selected from the Eromanga Basin in central Queensland (Figure 1); GSQ Blackall-1, GSQ Eromanga-1, GSQ Quilpie-1, GSQ Machattie-1, GSQ Maneroo-1, GSQ Thargomindah-3, and GSQ Tickalara-1 (these cores are stored in a Geological Survey of Queensland (GSQ) warehouse at Zillmere, Brisbane). Each core penetrates fluvial sediment of the Winton Formation and the underlying marine sediment of the Allaru and Mackunda Formations. Samples of approximately 5 cm³ each were selected for macrofossil preparation, based on a visual appraisal of the sediment. Each sample was numbered consecutively and prefixed with the first three letters of the bore core name. Stratigraphic details of samples which contained dicotyledonous macrofossils are given as

Table 1. Stratigraphic details of samples with dicotyledonous macrofossils.

| SAMPLE | DEPTH/M | FORMATION |
|--------|---------|-----------|
| MAC- 3 | 155.44 | Winton |
| MAC- 7 | 193.49 | Winton |
| MAC-11 | 319.7 | Mackunda |
| MAN- 6 | 28.8 | Winton |
| MAN- 7 | 29.4 | Winton |
| MAN- 8 | 29.7 | Winton |
| MAN- 9 | 29.8 | Winton |
| MAN-11 | 29.95 | Winton |
| MAN-12 | 30.0 | Winton |
| MAN-20 | 39.4 | Winton |
| MAN-22 | 42.0 | Winton |
| MAN-23 | 42.3 | Winton |
| MAN-28 | 80.4 | Winton |
| MAN-30 | 86.8 | Winton |
| MAN-34 | 161.6 | Mackunda |
| MAN-42 | 326.4 | Mackunda |
| THA-24 | 218.0 | Winton |
| THA-32 | 240.3 | Winton |
| THA-41 | 292.3 | Winton |
| THA-47 | 313.3 | Winton |

Table 1 (details of all samples are given in Pole and Douglas, 1999). Carbonaceous muds were preferred, sands were avoided unless they contained prominent carbonaceous horizons, and lignites were also generally avoided (previous experience and some tests indicated these usually do not preserve cuticle). Carbonaceous material was sparse in the marine sediment. Only two nearly intact leaves were recognised in hand specimen, the rest were small fragments of leaf lamina exhibiting some net venation or cuticle. In total, 235 samples were taken. Samples were numbered consecutively from the top of the core and given a prefix of the first three letters of the core name.

Most of the sample was processed for cuticle, leaving a small amount as a voucher specimen. Samples usually broke down into a sludge with the addition of warm water, but sometimes addition of a little hydrogen peroxide was needed. Sludge was washed through 500 and 125 μm mesh sieves, with most workable cuticle being retained on the 500 μm . Further clearing of cuticle involved increasing concentrations of warm peroxide. This treatment was controlled so that fragments retained veins or resin glands. Further clearing so that only cuticle remained used aqueous chromium trioxide. Any adhering silicates were removed

with hydrofluoric acid.

Samples were scanned under a binocular microscope, the dominant floristic components were estimated, and specimens were removed with tweezers for transmitted light microscopy (TLM) or (when sufficient extra material was available) scanning electron microscopy (SEM). Crystal Violet was used to stain when necessary.

There are insufficient data for the dicotydonous cuticles to formally diagnose new taxa and an informal system of nomenclature is used. Macrofossils and slides are catalogued with the prefix 'SL' and are stored in the Department of Botany, University of Queensland. Specimens mounted on Electron Microscope stubs are catalogued with the prefix 'S'. Specimens for TLM viewing were mounted on microscope slides with glycerine jelly, and those for SEM viewing on stubs with double-sided tape and coated with gold.

Results

Dicotyledon sp. A

Figures 2, 3

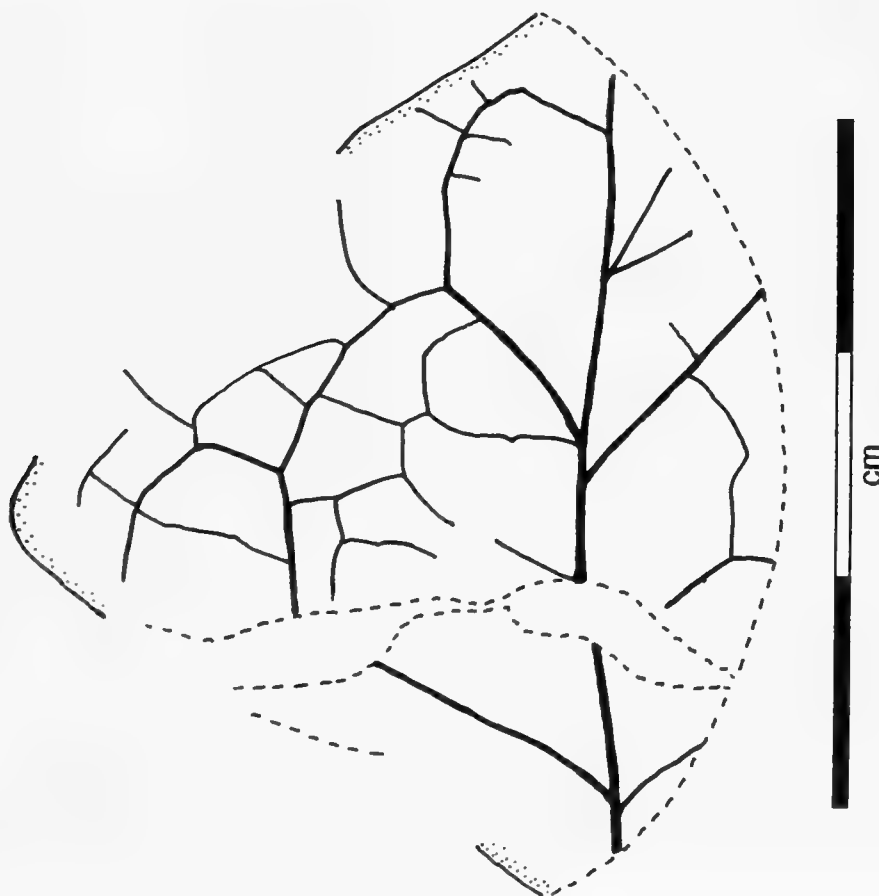


Figure 2. Dicotyledon sp. A, SL797. Line drawing of the only near-intact dicotydon fossil found. Stipple = margin, dashes = broken lamina. See Fig. 3 for photographs.

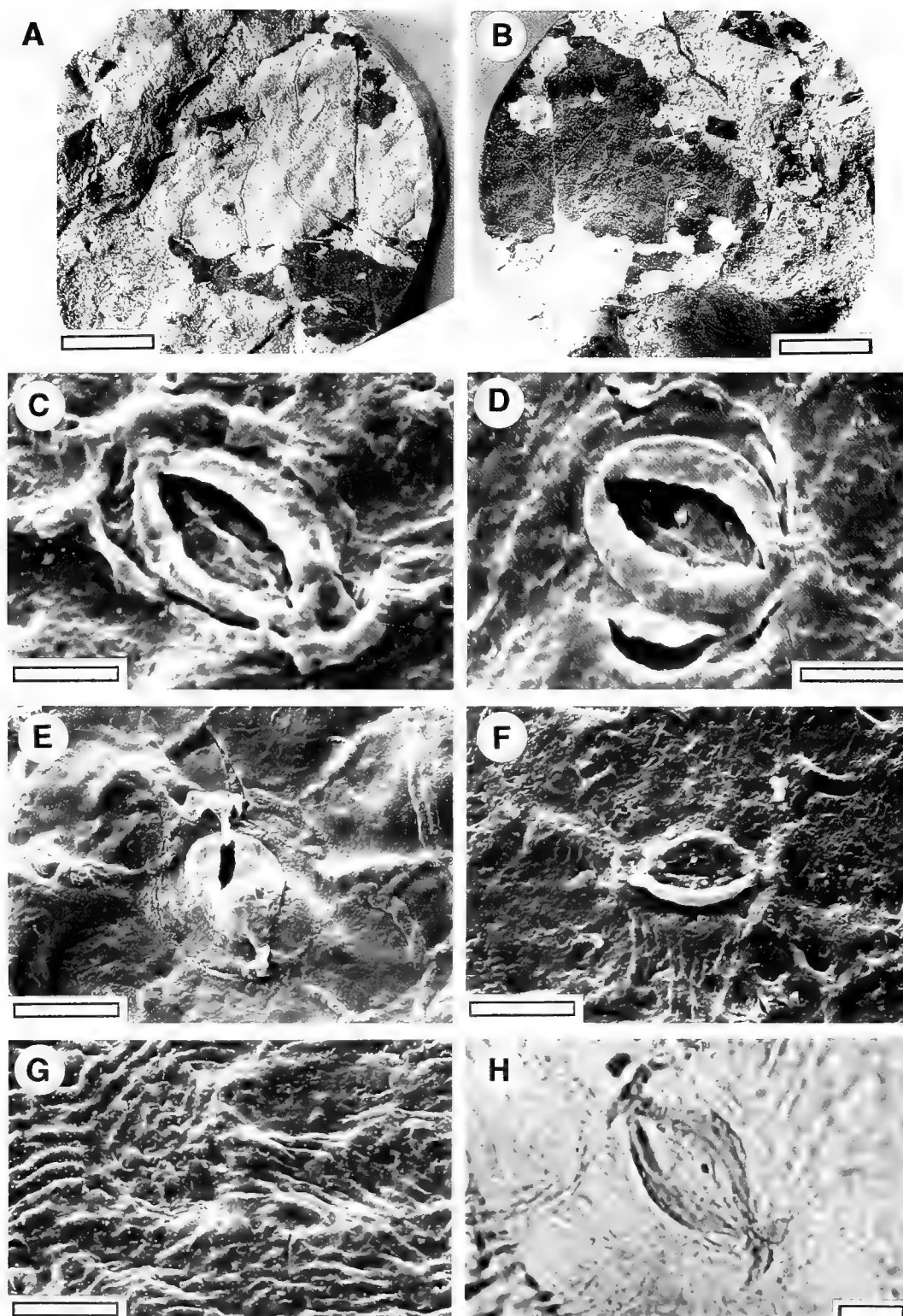


Figure 3. Dicotyledon sp. A. **A.** Intact leaf on bedding surface of drill core sample, SL797, scale: 1 cm. **B.** Counterpart of SL797, scale: 1 mm. **C.** SEM of outer surface of stoma, S761, scale: 10 μ m. **D.** SEM of outer surface of stoma, S763, scale: 10 μ m. **E.** SEM of inner surface of stoma, S763, scale: 20 μ m. **F.** SEM of outer surface of stoma showing ridges extending from lateral margin, S761, scale: 20 μ m. **G.** SEM of outer upper leaf surface showing ridges, S773, scale: 20 μ m. **H.** TLM of stoma, SL678, scale: 10 μ m.

Reference specimen.—SL797 (almost intact leaf on bedding surface, MAN-11).

Referred specimen and occurrence.—SL996; MAC-3 (dispersed cuticle).

Description.—Leaf lobed, length about 40 mm, width about 50 mm (midrib-margin 24 mm), hypostomatic; on abaxial surface stomatal orientation random; outline of guard cell pair ovate, outer stomatal ledge broad, T-piece thickenings at poles prominent; subsidiary cells not visible under

TLM, under SEM typically 6 isodiametric contact cells visible; cuticle very thin, epidermal cell flanges not visible under TLM; on surface ridges of cuticle sometimes present over outer walls of guard cells, also bands of fine ridges prominent, extending laterally from guard cells; glabrous; adaxial surface epidermal cell flanges visible under TLM, isodiametric, polygonal, straight-walled; finely and evenly ridged on surface; glabrous.

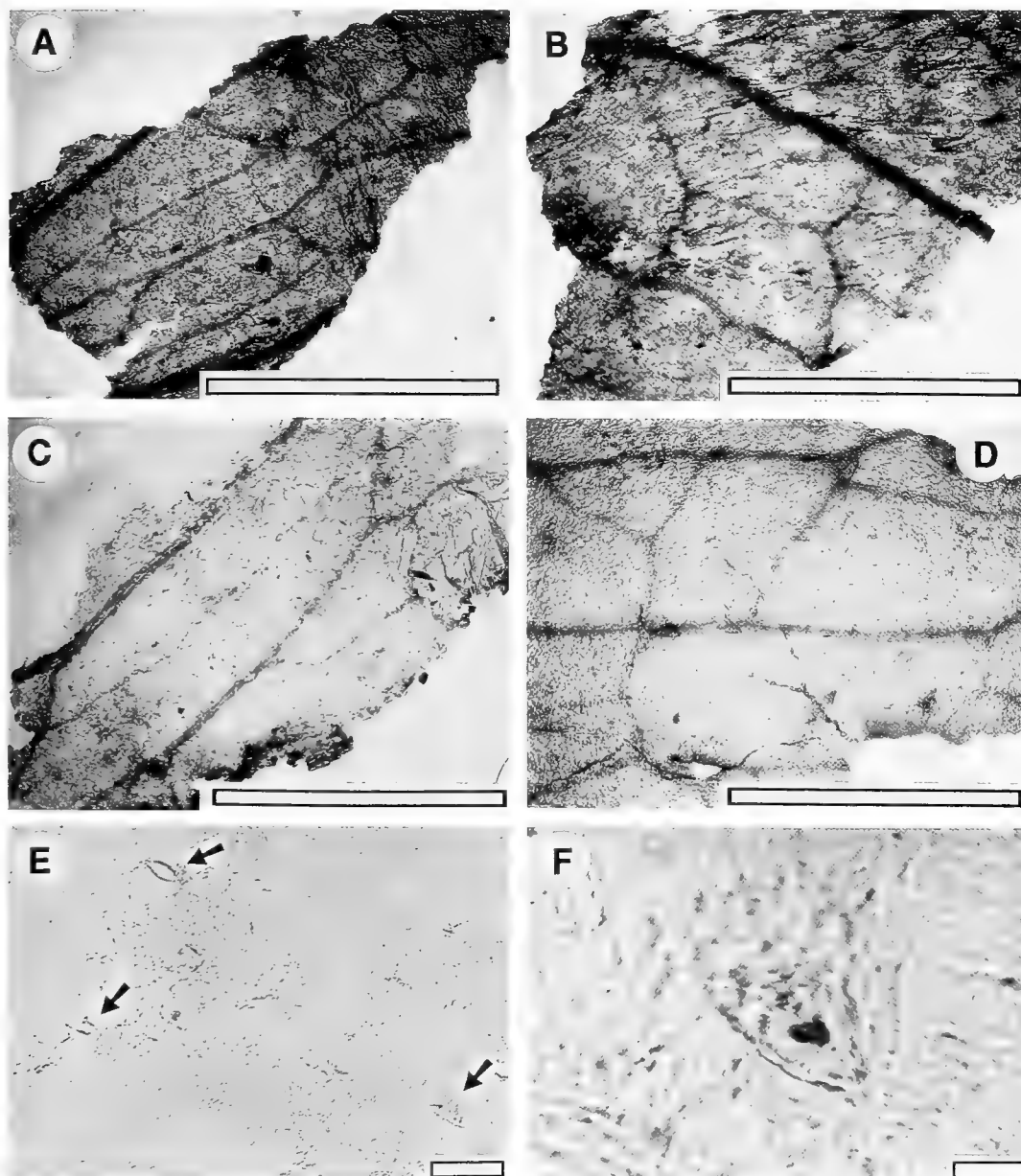


Figure 4. Dicotyledon sp. B. **A–D.** TLMs of leaf fragments with net-venation, scale: 1 mm. **A.** SL776. **B.** SL777. **C.** SL774. **D.** SL773. **E.** TLM of cuticle showing widely separated, aligned stomata (arrowed), SL787, scale: 50 µm. **F.** TLM detail of single stomate, note narrow, elliptical rim, SL787, scale: 10 µm.

Dicotyledon sp. B

Figure 4

Reference specimen.—SL787 (dispersed cuticle, MAN-23).

Referred specimens and occurrence.—SL997, MAN-9; SL774, MAN-11; SL773, MAN-20; SL771, MAN-22; SL776,

SL777, MAN-23; SL788, MAN-34.

Description.—Leaf shape unknown, small fragments of lamina exhibit net-venation; stomata scattered, infrequent, visible under TLM as very thin, aligned (at least over small areas), elliptical, outer stomatal ledges; cuticle otherwise very thin, no clearly distinguished subsidiary cells, epidermal cell flanges generally not visible, isodiametric, smooth,

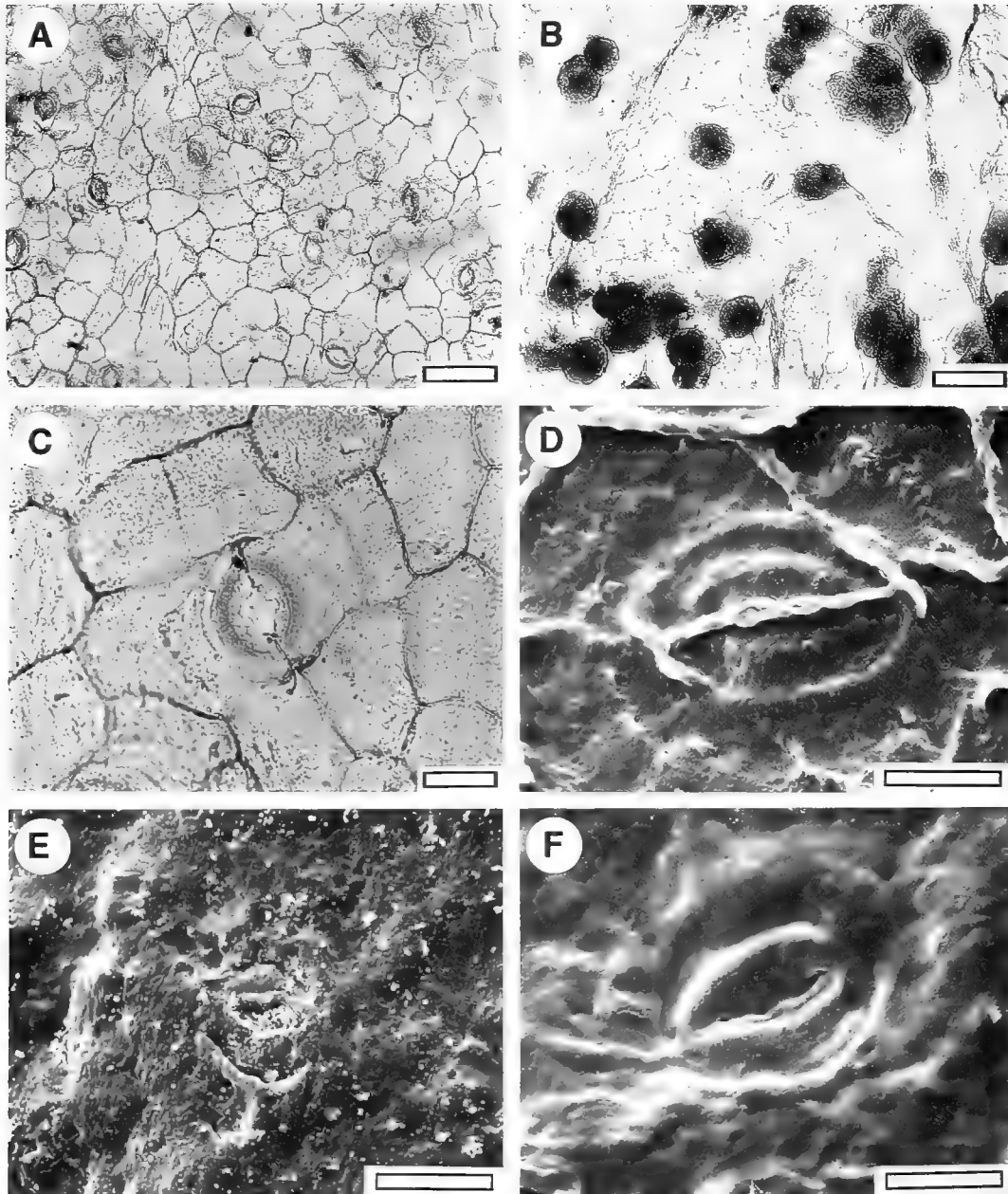


Figure 5. Dicotyledon sp. C. **A.** TLM, SL738, scale: 100 µm. **B.** TLM with numerous dark resin bodies still attached, SL735, scale: 100 µm. **C.** TLM of single stoma, SL738, scale: 25 µm. **D.** SEM of inner surface of single stoma, note T-piece thickening, S765, scale: 20 µm. **E.** SEM of outer surface of single stoma, S759, scale: 20 µm. **F.** SEM of outer surface of single stoma, S765, scale: 20 µm.

slightly thicker over veins; glabrous.

Dicotyledon sp. C

Figure 5

Reference specimen.—SL738 (dispersed cuticle, MAN-30).

Referred specimens and occurrence.—SL731, MAN-6; S760, MAN-7; SL733, MAN-8; S765, MAN-9; S759, MAN-11; SL735, MAN-12; SL739, MAN-42; SL676, THA-32.

Description.—Stomatal orientation random, outer stomatal ledges broad; distinct, thin T-piece thickenings at guard cell poles; peristomatal thickening sometimes present; no clear or consistent subsidiary cell arrangement but lateral contact cells often divided tangentially to give irregular-shaped subsidiary cells; normal epidermal cells polygonal, smooth; major veins (midrib?) visible as more elongate, rectangular epidermal cells; outer cuticular surface smooth; typically glabrous but sparse poral trichome bases sometimes present; resin bodies from within leaf lamina often adhering to

cuticle (e. g. SL735).

Note.—The resin bodies are similar to those widespread throughout the extant magnoliids (Metcalf, 1987; pers. obs.).

Dicotyledon sp. D

Figure 6

Reference specimen.—SL676 (dispersed cuticle, THA-32)

Referred specimens and occurrence.—SL895, MAC-7; SL677, THA-41

Description.—Stomatal distribution over leaf unknown; stomata randomly oriented; guard cell pair outline ovate, central portion covered by broad outer stomatal ledge; T-piece thickenings present at guard cell poles; subsidiary cell pattern variable, polar and lateral subsidiary cells typically recognisable, but sometimes not; lateral subsidiary cells present in up to three layers (including the hexacytic arrangement of van Cotthem, 1970b), apparently formed by

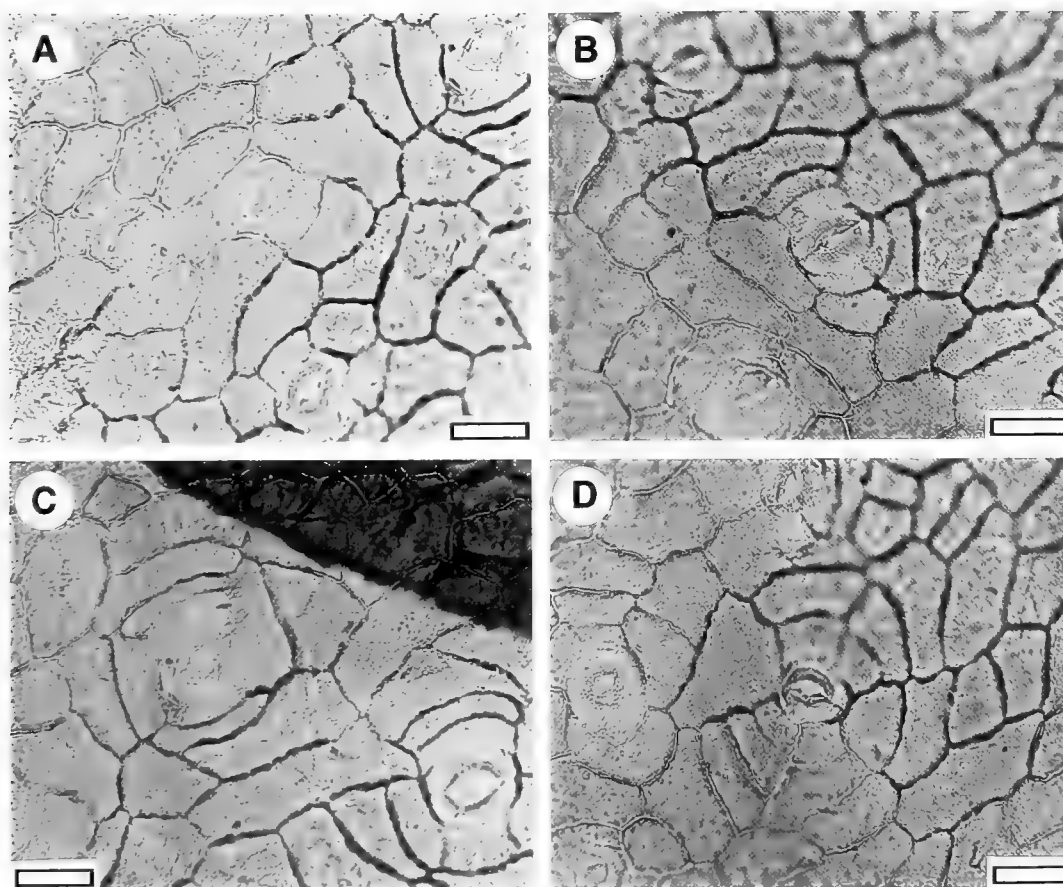


Figure 6. *Dicotyledon sp. D*, all SL676, TLMs of stomata of varying type, scale: 25 μ m. **A.** Stomata with single lateral subsidiary cells on either side, some have divided radially. **B.** Stoma with 3 lateral subsidiary cells on one side, and two on the other which have both divided radially. **C.** Stomata with two lateral subsidiary cells. **D.** Stoma with six lateral subsidiary cells on one side.

elongate, tangential divisions of contact cells, sometimes also radially divided (i. e. giving six lateral subsidiary cells on one side of stoma); polar subsidiary cells irregular (probably just unmodified contact cells) or sometimes elongate, forming from tangential division of contact cell; veins not reflected in epidermal cells; glabrous.

Dicotyledon sp. E

Figure 7

Reference specimen.—SL772 (only specimen, small leaf with apex and base missing, two teeth present, MAN-34).

Description.—Leaf toothed or lobed, preserved lamina length 6 mm, up to 4 mm wide, teeth/lobes 0.8 mm wide and high; first order venation externodromous; tooth vascularisation central; stomata visible only as thin, elliptical outer stomatal ledges; aligned with midrib when close, or aligned with lateral venation further away; resin bodies numerous within lamina.

Dicotyledon sp. F

Figure 8

Reference specimen.—SL678 (dispersed cuticle, only

specimen, THA-24).

Description.—Stomatal distribution over leaf unknown; stomata randomly oriented; outer stomatal ledges prominent, elliptical, sometimes narrowing abruptly before poles; prominent T-piece thickenings at stomatal poles; subsidiary cells not visible; cuticle very thin, epidermal cell flanges not visible in TLM, faint under SEM; outer epidermal surface ornamented by swirling bands of fine ridges sometimes starting at right angles from lateral subsidiary cells, but also with no consistent orientation to stomates; sometimes peristomal ridges present along edges of guard cells.

Note.—The general appearance of the cuticle, particularly the surface ornamentation, appearance of the outer stomatal ledge, and the prominent T-piece thickenings are comparable with two extant genera of the Illiciales, *Kadsura* (Schisandraceae; cf. fig. 24F Metcalfe, 1987) and *Illicium* (Illiciaceae; cf. fig. 22B Metcalfe, 1987), suggesting a relationship with this order. The same features are comparable with *Eucalyptophyllum oblongifolium* Fontaine from the Potomac Group, which was suggested by Upchurch (1984, p. 544 and cf. his figure 7) to represent "an extinct group of at least ordinal rank... that is related in some way to Chloranthaceae and Illiciales."

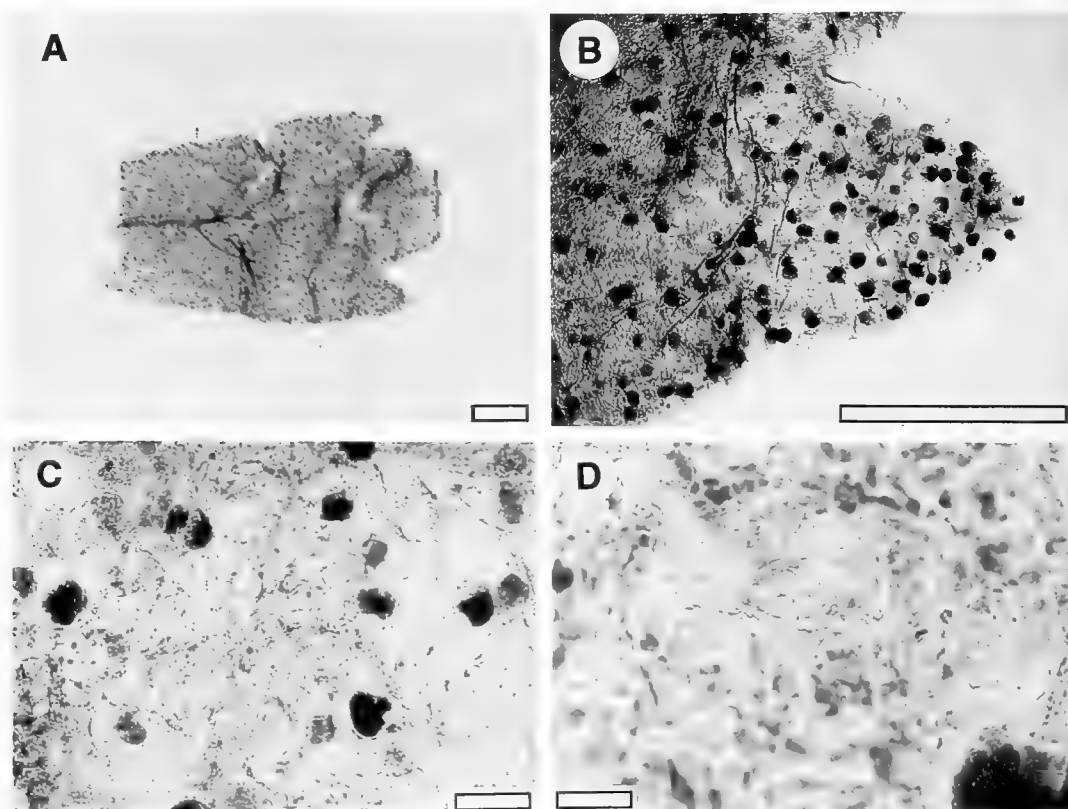


Figure 7. *Dicotyledon* sp. E, all SL772. **A.** TLM of complete specimen, note teeth and broken apex, scale: 1 mm. **B.** TLM detail of tooth showing numerous resin bodies, scale: 1 mm. **C.** TLM detail showing stoma (arrowed) and resin bodies, scale: 100 µm. **D.** TLM detail of single stoma, scale: 25 µm.

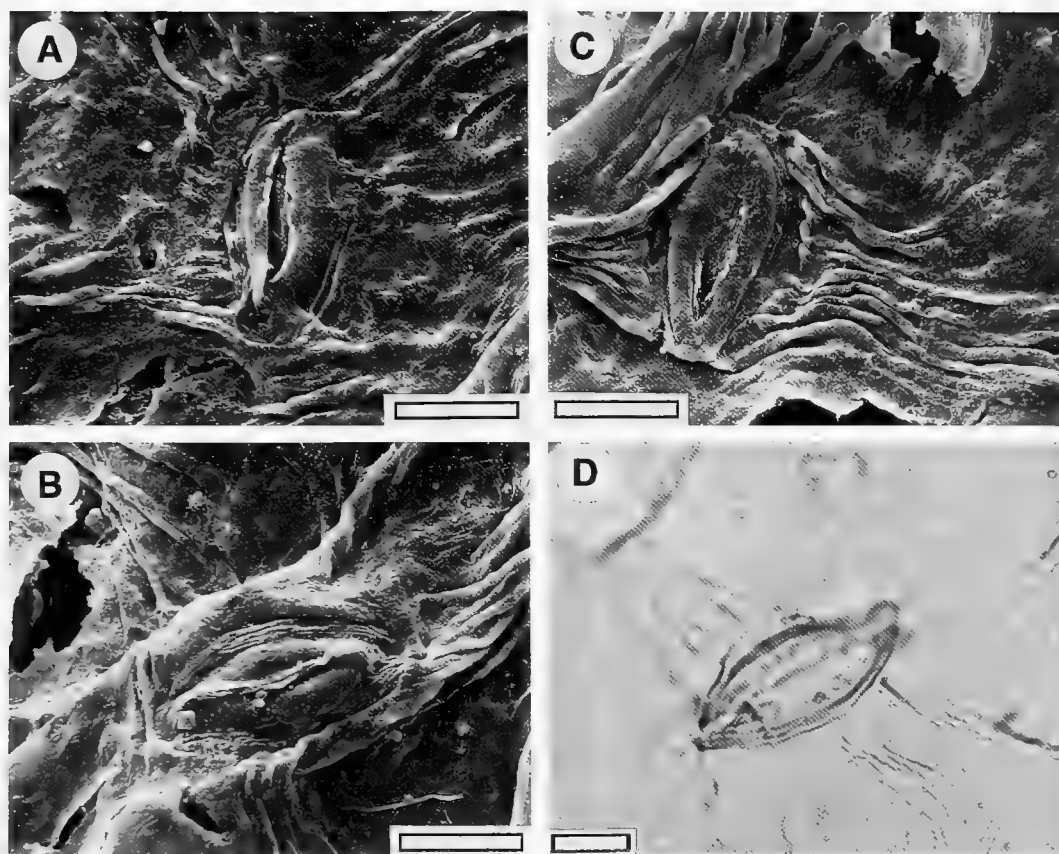


Figure 8. *Dicotyledon* sp. F. **A–C.** SEMs of outer surface of single stoma, all S764, scale: 20 μ m. **D.** TLM of outer surface of single stoma, SL768, scale: 10 μ m.

Dicotyledon sp. G

Figure 9

Reference specimen.—SL894 (dispersed cuticle, only specimen, MAC-11).

Description.—Stomatal distribution over leaf unknown; stomata randomly oriented; normal stomata sunken under and occluded by frilled, radiating rim of cuticle; giant stomata common, exposed, with thin, elliptical, outer stomatal ledge, surrounded by low tangentially oriented ridges; major veins only reflected in epidermal cells; glabrous.

Dicotyledon sp. H

Figure 10A, B

Reference specimen.—SL987 (dispersed cuticle, only specimen, MAC-3).

Description.—Stomatal distribution over leaf unknown; stomata randomly oriented; normal stomata dense; outer stomatal ledge broad, narrowing at poles, not extending full length of guard cells; moderate T-piece thickenings at stomatal poles; peristomal thickenings sometimes present; giant stomata present; no distinct subsidiary cells; contact

cells of separate stomata often abut, sometimes shared; outer stomatal ledge wide; normal epidermal cell shape irregular, rounded, generally slightly elongate; fine ridges on outer surface of cuticle oriented parallel to stomatal pore; major veins reflected in more rectangular, slightly papillate epidermal cells; glabrous.

Dicotyledon sp. I

Figure 10C, D

Reference specimen.—SL737 (only specimen, poorly preserved leaf fragment near apex, bases of teeth present, MAN-28).

Description.—Leaf margin with small teeth; stomatal distribution over leaf hypostomatic; stomata randomly oriented; guard cell pair outline ovate; outer stomatal ledge narrow, not extending full length of guard cells; no obvious subsidiary cells; epidermal cell flanges prominent; normal outline polygonal, isodiametric; midrib reflected in epidermal cells.

Dicotyledon sp. J

Figure 10E, F

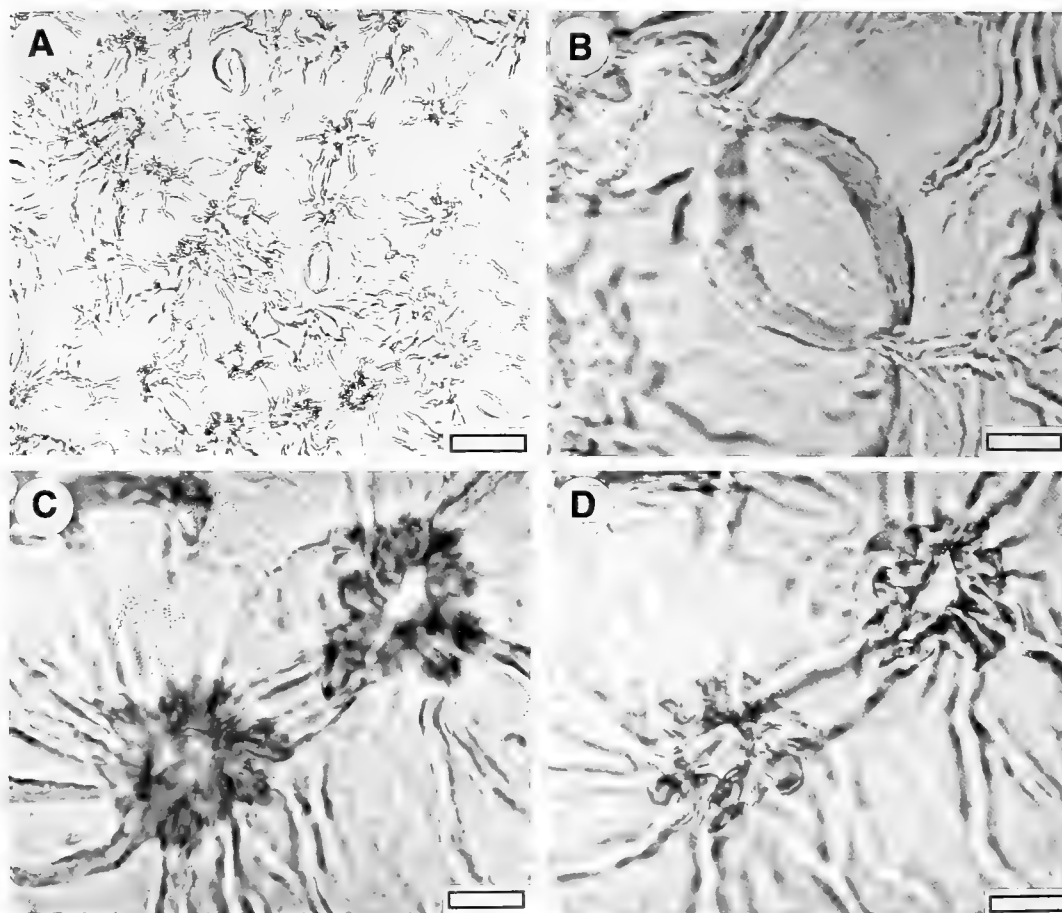


Figure 9. Dicotyledon sp. G, all SL894. **A.** TLM showing exposed giant stomata and normal stomata obscured by cuticle ridges, scale: 50 μ m. **B.** TLM detail of giant stomata, scale: 10 μ m. **C, D.** TLM of two normal stomata. **C.** Lower focus. **D.** Higher focus, scale: 10 μ m.

Reference specimen.—SL679 (dispersed cuticle, only specimen, THA-47).

Description.—Stomatal distribution over leaf hypostomatic; on abaxial surface stomata generally aligned but some oblique, striations aligned with stomates, elliptical, thickened outer stomatal ledge, epidermal cell flanges not visible under TLM; glabrous; adaxial surface also with parallel striations, glabrous.

Identification

Worldwide, most described angiosperm leaf fossils of Albian-Cenomanian age are impressions only, lacking cuticle. However, in this study, although cuticular preservation is good, most material is found as small, dispersed fragments in amongst a large amount of coniferous material (the chances of a bore core sampling a complete leaf are slim). This situation is frustrating, as a combination of gross leaf morphology and venation combined with anatomical detail would be a great help in identification. Nevertheless, these

are the best preserved angiosperms from the Australian Cretaceous to date, and the cuticle is amongst the oldest from angiosperms in the world. The few Cenomanian records of cuticle include Upchurch (1984, 1995) and Kvacek (1983, 1992), and for the Albian that of Crane *et al.* (1993).

The current knowledge of mid-Cretaceous angiosperms is based on pollen, flowers, and leaves, and includes several identifications of extant taxa. For instance, the Upper Albian Potomac Group of North America has yielded reproductive material regarded as of probable chloranthoid, hamamelididean, magnoliidean, platanoid, and rosidae affinities (Friis *et al.*, 1986; Crane *et al.*, 1986). The Cenomanian, or possibly late Albian Dakota Formation has yielded possible Magnoliales (Dilcher and Crane, 1984). These inferred affinities are at high taxonomic levels (but have still raised dispute, e. g. Hughes, 1994), nevertheless they may form a starting point for comparing fossil cuticle. Upchurch and Wolfe (1993) summarised the data from Cretaceous leaf fossils, including the latest Albian to middle Cenomanian period. Similar to the reproductive material

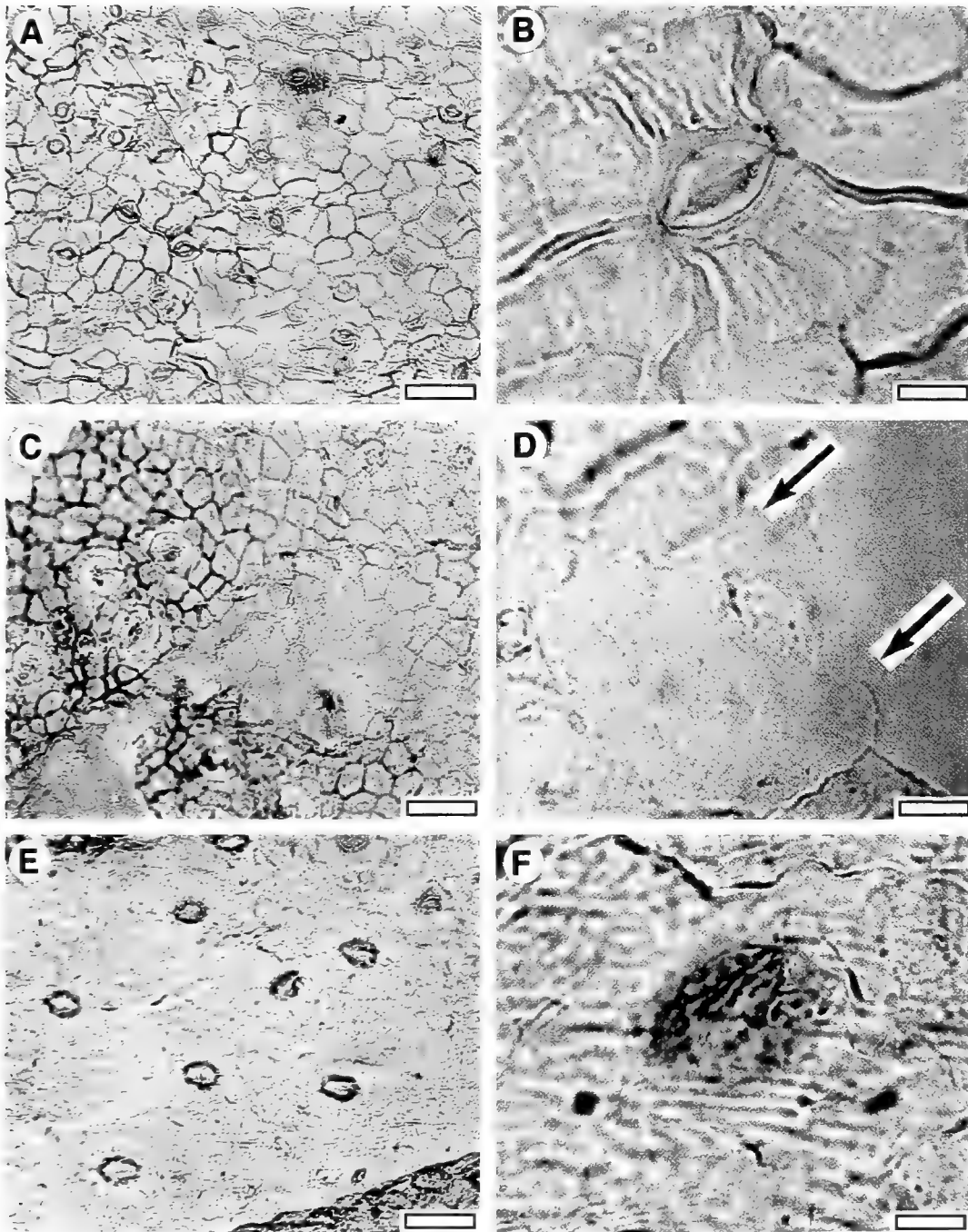


Figure 10. A, B. *Dicotyledon* sp. H, both SL987. A. Scale: 50 μ m. B. Scale: 10 μ m. C, D. *Dicotyledon* sp. I, both SL737. C. scale: 50 μ m. D. Arrows point to opposite poles of a single stoma, scale: 10 μ m. E, F. *Angiosperm* sp. J, both SL679. E. Scale: 50 μ m. F. Scale: 10 μ m.

the affinities included the Magnoliales, Laurales, Hamamelidales (aff. to Platanaceae) and the Rosidae. Thus, even at this relatively early stage, several of the major clades of angiosperms recognised by Chase *et al.* (1993), were present.

Despite having some indication of 'where to look' for the affinities of the Eromanga material, taxonomic placement is far from obvious. For one taxon (Dicotyledon sp. F) an affinity with the Chloranthaceae and Illiciales has been suggested, but for the others their identity remains completely unknown. This situation may result from a combination of inadequate material for comparison with extant plants as well as the likelihood that plants of this age had combinations of cuticle characters unknown today (e. g. Upchurch, 1984). Certainly none of the cuticle has any of the characteristic features of extant Australian families such as Lauraceae, Myrtaceae, or Proteaceae which are well known in the Tertiary record (and which would not be expected for this time). *Platanus* or extinct relatives were widespread in the mid-Cretaceous, including New Zealand (Pole, 1992), but none of the fossil cuticle is comparable to extant *Platanus* (documented by Brett, 1979). However, cuticle of Albian *Sapindopsis*, regarded as Platanaceae by Crane *et al.* (1993), compares favourably with Dicotyledon spp. A, F, and H in the presence of surface striations and form of the outer stomatal ledge. Curiously, where subsidiary cells can be seen, none of the Eromanga cuticle shows the paracytic subsidiary cell arrangement which is common in extant plant families often regarded as 'primitive', i. e. the 'paleoherbs' of Donoghue and Doyle (1989). However, Upchurch (1984) reported a plastic, variable condition of the subsidiary cell arrangement for Lower Cretaceous Potomac Group cuticles and suggested it to be an even more primitive style, although Baranova (1992) remarked that several extant taxa also show such plasticity. This plasticity is shown by Dicotyledon sp. D from the Eromanga. As for whole leaf form, the single larger leaf fragment of Dicotyledon sp. A is not comparable with any of the material illustrated by McLoughlin *et al.* (1995) from younger Winton Formation deposits, although its lobed form would not be out of place in their assemblage.

Distribution

All samples containing dicotyledonous fossils come from the Winton Formation, except three (MAC-11; MAN-34, 42), which came from the underlying Mackunda Formation.

Angiosperm cuticle was not found in sandy samples. This could be a result of its not surviving in that environment (i. e. fluvial abrasion destroyed the cuticle), or because physical distortion by sand grains during compaction may have rendered the cuticle unrecognisable. It may also be a real absence, suggesting angiosperms were typically absent along relatively high-energy sedimentary environments such as river margins or levees. However, the three Mackunda Formation samples come from marine sediments to where the fossils contained must have been transported by fluvial activity. Out of the 144 fossiliferous samples which were fine-grained or muddy, only 20 of them contained dicotyledonous remains and these were restricted to three of the

seven cores; GSQ Machattie-1, GSQ Maneroo-1, and GSQ Thargominda-3 (Appendix 1). This suggests that, at least in the lower-energy floodplain environments, dicotyledons were either patchy in their distribution, or were relatively small plants, producing little biomass. They were evidently a small component of what was, on a regional scale, an overwhelmingly gymnosperm (mostly conifer) dominated flora (Pole, in prep.). Burger (1990), on the basis of palynological data, also concluded the angiosperms were patchily distributed. One sample (MAC-11) comes from a thin unit of Winton Formation bounded above and below by marine sediments which probably accumulated very close to sea level, perhaps as a delta lobe. The other samples are interpreted as accumulating essentially in an overbank/floodplain environment (see facies analysis of the Eromanga core by Fielding, 1992).

Although no dicotyledon fossils were recovered from coal, some samples were stratigraphically close. Sample THA-47 comes from a mud immediately below the prominent coal seam of Thargomindah-3. Samples MAN 6, 8, 9, 11, 12 (closely spaced, all coming from a 4.5 m-thick muddy unit) are close to the prominent coal seam of Maneroo-1 but separated from it by a 3.5 m-thick sandy bed. The most reasonable assumption is that the angiosperms grew in clastic swamps, but growth on sandy levees or in coal swamps cannot be discounted. The plants were probably woody rather than herbaceous, as herbs are unlikely to become fossilised and their very delicate cuticle would not be expected to be preserved, or to survive the preparation process. Even so, some of the fossil cuticle is notably thin, consistent with understorey plants or deciduousness.

Summary

Latest Albian-earliest Cenomanian assemblages from the Eromanga Basin, Australia include sporadic fragments of dicotyledonous leaf cuticle, and rare semi-intact leaves. Ten types can be distinguished with the affinities of at least one possibly being with the Chloranthaceae and Illiciales.

Acknowledgements

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A new pseudorthoceratid cephalopod from the Kazanian (middle Late Permian) of Japan

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Abstract. A new cephalopod species, *Dolorthoceras nakazawai* (Orthocerida: Pseudorthoceratidae), is described from the Permian Mizuyagadani Formation, Central Japan. Its Kazanian age, based on a fusulinid species, makes this the youngest record of *Dolorthoceras*. This is the first undoubted occurrence of the genus in Japan.

Key words: *Dolorthoceras nakazawai* sp. nov., Orthocerida, Mizuyagadani Formation, Permian, Kazanian

Introduction and geologic setting

A new pseudorthoceratid cephalopod species, *Dolorthoceras nakazawai*, is described from a float block of limestone in the upper reaches of Ichinotani Valley in the Fukuji area, Gifu Prefecture, Central Japan. The vicinity of the collecting site is underlain by the Mizuyagadani Formation (Igo, 1956), which consists mostly of clastic sediments and has a "lenticular" limestone in its upper part (see fig. 2 in Niko *et al.*, 1987). The cephalopod-bearing limestone consists of bioclastic wackestone and has a characteristic appearance that is dark gray micrite, with sporadic crinoid fragments as the main allochemical constituent, and is identical in lithology with the "lenticular" limestone noted above. With the exception of apparently reworked fossils, the age of this formation has been discussed on the basis of foraminifers (Okimura *et al.*, 1984), radiolarians (Niko *et al.*, 1987; Umeda and Ezaki, 1997), corals (Kamei, 1957; Igo, 1959), brachiopods (Kamei, 1957) and cephalopods (Niko and Nishida, 1987; Nishida and Niko, 1989). Among them, radiolarians in tuffaceous mudstone and acidic tuff range from Sakmarian (middle Early Permian) to Midian (middle Late Permian), and ammonoids reported by Nishida and Niko (1989) are the only fossils known from the "lenticular" limestone excepting crinoid fragments. Although the precise age of the limestone is a pending question, we found the index fusulinid *Parafusulina* cf. *kaerimizensis* (Figure 1), associated with the pseudorthoceratid cephalopod *Dolorthoceras nakazawai* sp. nov., from the same locality and in limestone of similar lithology (but from another float block). It is possible that this limestone is a redeposited olistolith or has been introduced by faulting, but its age can be

determined by the presence of *Parafusulina* cf. *kaerimizensis*. Based on the assembled evidence, we conclude that the specimen of *D. nakazawai* was derived from the "lenticular" limestone in the Mizuyagadani Formation, and that its age is Kazanian (middle Late Permian).

The abbreviation UMUT for the repository stands for the University Museum of the University of Tokyo.

Systematic paleontology

Order Orthocerida Kuhn, 1940

Superfamily Pseudorthocerataceae Flower and Caster, 1935

Family Pseudorthoceratidae Flower and Caster, 1935

Subfamily Spyroceratinae Shimizu and Obata, 1935

Genus *Dolorthoceras* Miller, 1931

Type species.—*Dolorthoceras circulare* Miller, 1931.

Dolorthoceras nakazawai sp. nov.

Figure 2

Diagnosis.—Species of *Dolorthoceras* with circular shell cross section; sutures oblique, attaining 16° to rectangular direction of shell axis; siphuncular position nearly central with asymmetrical septal necks; cameral deposits form circum-siphuncular ridge and mamiform growth; endosiphuncular deposits form thick lining on ventral siphuncular wall.

Description.—Orthoconic shell with circular cross section, reaches 7.4 mm in diameter near adoral end; shell expansion moderate with approximately 5° angle; shell surface

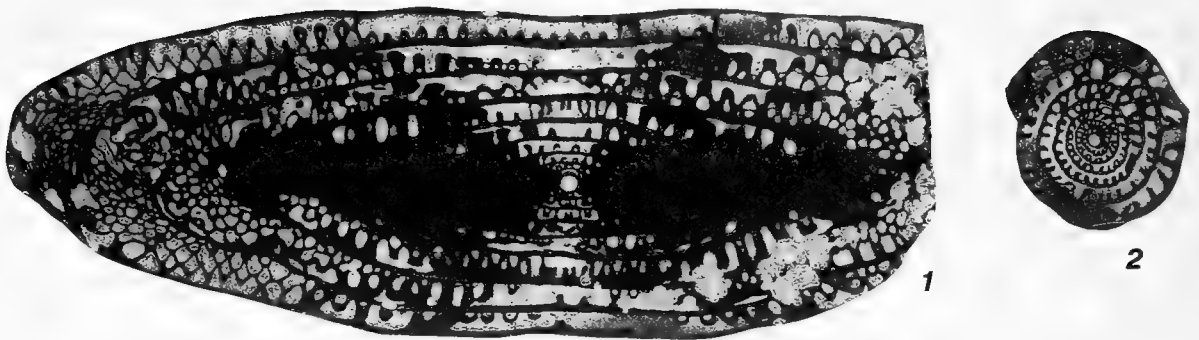
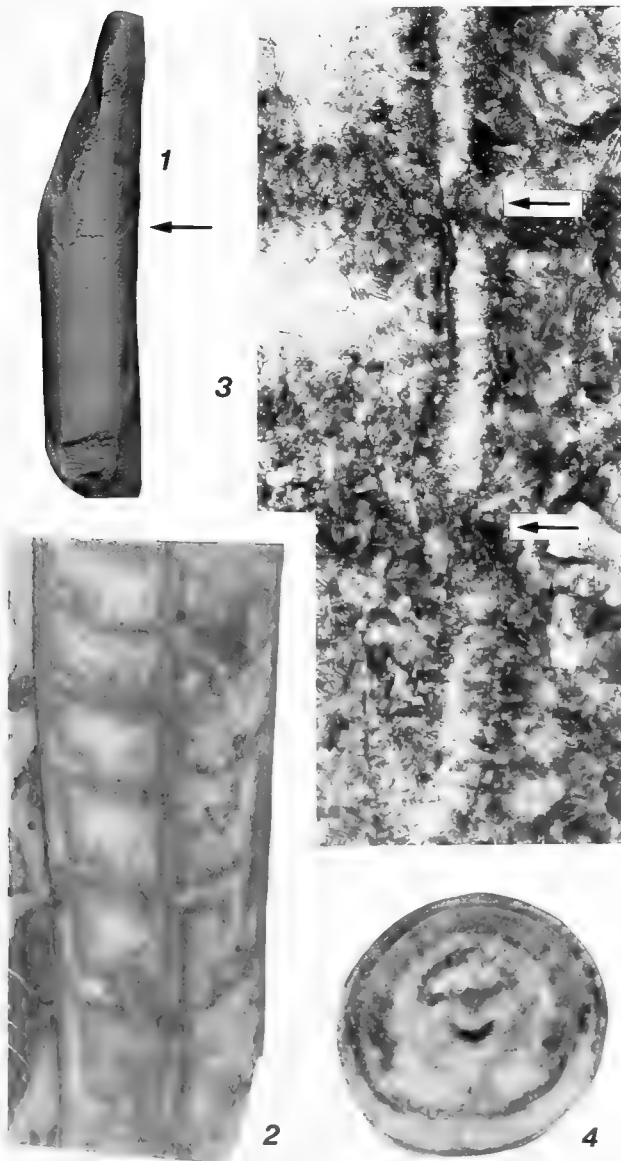


Figure 1. *Parafusulina* cf. *kaerimizensis* (Ozawa) from the Fukuji area, thin sections. 1. Axial section, $\times 10$. 2. Sagittal section, $\times 10$.



smooth, obvious ornamentation not recognized. Sutures not observed, but with relatively strong obliquity, ranging from 12° to 16° to rectangular direction of shell axis, as recognized in dorsoventral section, toward aperture on venter; septal curvature moderate to relatively deep, steeper in venter than dorsum; camerae relatively long for genus in apical phragmocone, with maximum width/length ratio 1.7 at shell diameter approximately 5.4 mm, being increased to 3.3 near adoral end. Siphuncle nearly central in position; septal necks asymmetrical in form, suborthochoanitic to rarely cyrtochoanitic in ventral siphuncular wall, and strongly curved cyrtochoanitic in dorsal siphuncular wall; length of septal necks short, ranging from 0.31 mm to 0.56 mm; brims short with length nearly equal to septal necks in adoral and ventral siphuncular wall, but in other portions they are shorter than septal necks; adnation area very narrow; connecting rings weakly inflated, subcylindrical with constrictions at septal foramina; ratio of maximum external diameter of connecting ring/corresponding shell diameter is approximately 0.2. Ventral cameral deposits well developed, episepal-mural or episepal and mural on rare occasions, always form circumsiphuncular ridge and mamiform growth; dorsal cameral deposits episepal-mural indicating L-shaped longitudinal profile, relatively thin. Endosiphuncular deposits restricted to ventral siphuncular wall, where they form a thick lining with crescentic transverse profile.

Discussion.—With the exception of *Dolorthoceras*, the relatively simple shell morphology of the present species has much in common with Late Paleozoic *Spyroceratinae* such as *Adnatoceras* (Flower, 1939), *Euloxoceras* (Miller *et al.*, 1933), *Mitorthoceras* (Gordon, 1960) and *Shikhanoceras* (Shimanskiy, 1954). However, the combination of an uncompressed shell with a smooth surface, the very narrow adnation area and the short brims confirms the assignment

Figure 2. *Dolorthoceras nakazawai* sp. nov., holotype, UMUT PM 27826, from the Fukuji area. 1. Ventral view, $\times 2$. 2. Dorsoventral thin section, venter on right, $\times 5$. 3. Dorsoventral thin section, showing the details of the siphuncular structure. Arrows indicate septal necks, $\times 14$. 4. Transverse polished section at position indicated by arrow in Figure 2.1, venter down, $\times 5$.

of the species to *Dolorthoceras*, which was proposed by Miller (1931) from the Upper Carboniferous in the Aghil-Depsang (Central Range) of Central Asia. Its previously known range was Early Devonian to Early Permian, with an upper limit represented by two Artinskian species from the Urals, namely *Dolorthoceras siphocentrale* (Krotov, 1885, pl. 1, fig. 3; Shimanskiy, 1954, pl. 1, figs. 11, 12a, b) and *D. stiliforme* Shimanskiy (1948, figs. 1a, b; Shimanskiy, 1954, pl. 1, figs. 1–10, pl. 2, figs. 1–6). Thus, the present discovery of *Dolorthoceras* in the Mizuyagadani Formation extends the stratigraphic range of this genus upwards to the Kazanian.

The somewhat similar *Dolorthoceras stiliforme* is distinguished from *D. nakazawai* sp. nov. in having a subcentral siphuncular position, the usually simple mural cameral deposits and the unfused endosiphuncular deposits. Niko and Nishida (1987, fig. 3.3–3.5) assigned a specimen from the same formation to an indeterminate genus and species of the Pseudorthoceratidae having the surface annulation clearly separate from *D. nakazawai* at the generic level.

A poorly preserved specimen of *Dolorthoceras*? sp. from the Early Carboniferous Hikoroichi Formation in the southern Kitakami Mountains (Niko, 1990) was the only record of this genus in Japan until the present report.

Material.—Holotype and only known specimen, UMUT PM 27826, is an incomplete phragmocone 37.2 mm in length.

Etymology.—The specific name honors Dr. Keiji Nakazawa, in recognition of his contributions to the study of Permian mollusks.

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Early Carboniferous miospores from the southern Kitakami Mountains, northeast Japan

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Abstract. The first authenticated Early Carboniferous miospores in Japan are described from the upper part of the lower Hikoroichi Formation (HK2 Member) in the Hikoroichi area, southern Kitakami Mountains, northeast Japan. The stratigraphically significant miospores are *Auroraspora* sp. cf. *A. macra*, *Crassispora trychera*, *Schopfites* sp., *Spelaeotriletes crustatus*, and *S. sp. cf. S. pretiosus*, which suggest a late Tournaisian to early Viséan age and the “*Vallatisporites* Microflora” provincialism.

Key words: Hikoroichi Formation, late Tournaisian to early Viséan, miospores, southern Kitakami Mountains

Introduction

Because of their poor preservation and scarcity late Paleozoic plant fossils in Japan have aroused little interest among Japanese paleontologists. Microfloral research in the Upper Paleozoic of Japan is even more limited as it was commonly believed that spores and pollen are only preserved in terrestrial environments. However, there are many cases from around the world of Upper Paleozoic terrestrial microflora preserved in marine sediments, where they are significant to both stratigraphy and phytogeography (Sullivan, 1965; Yang, 1999). Prior to this paper there have been no reports of late Paleozoic miospores from Japan, although Takahashi and Yao (1969) reported the occurrence of problematic Permian plant microfossils from a sandstone block of the Jurassic melange in the Harayama area, Mino Belt, southwest Japan.

The Hikoroichi Formation is a Lower Carboniferous (Tournaisian and Viséan) formation, distributed in the Hikoroichi area, western part of the southern Kitakami Mountains (Figure 1). The Hikoroichi Formation overlies, with angular unconformity, the Middle Devonian Nakazato Formation (Okubo, 1951; Minato *et al.*, 1979), and is in turn overlain conformably by the Lower Carboniferous (Upper Viséan) Onimaru Formation (Mori and Tazawa, 1980; Tazawa, 1981, 1984b; Kawamura, 1983). According to Tazawa (1984b), the Hikoroichi Formation consists mostly of sandstone, with a basal conglomerate and intercalations of shales, acidic to intermediate tuffs and limestones, 560 m in total thickness, and is subdivided into the following four members in ascending order: (1) HK1 Member, sandstone

dominant, 164 m thick, (2) HK2 Member, shale dominant, 102 m thick, (3) HK3 Member, basic to intermediate tuff dominant, 114 m thick, (4) HK4 Member, sandstone dominant, 180 m thick (Figure 2).

The miospores, described below, are from samples collected from the middle horizon of the HK2 Member at the Onimaru Quarry in the Hikoroichi area (Figures 1, 2). All the specimens are housed in the Department of Geology, Faculty of Science, Niigata University with the registered number (NU-P1–NU-P5). The other fossils, corals (Kato *et al.*, 1989), bryozoans (Sakagami, 1989), brachiopods (Tazawa, 1984a, 1985, 1989), gastropods (Kase, 1988), cephalopods (Niko, 1990) and trilobites (Kaneko, 1989) were collected from almost the same horizon in the same quarry. However, the plants alone were collected from the lowermost part of the HK3 Member in the same locality (Asama *et al.*, 1985, 1989). These fossils from the HK2 and HK3 Members of the Hikoroichi Formation in the Onimaru Quarry are summarized in Table 1.

Miospore preservation and processing technique

The extraction of palynomorphs from Japanese Paleozoic rocks is difficult. Lithologies suitable for the preservation of palynomorphs make up only about 10% of the Hikoroichi Formation (see Figure 2). Further, the miospores preserved in the shales of the Hikoroichi Formation are rather dark and thermally mature and need strong oxidation after conventional palynological processing (Wood *et al.*, 1996). Processing of samples from the Hikoroichi Formation involved crushing the samples to pea size or even finer and

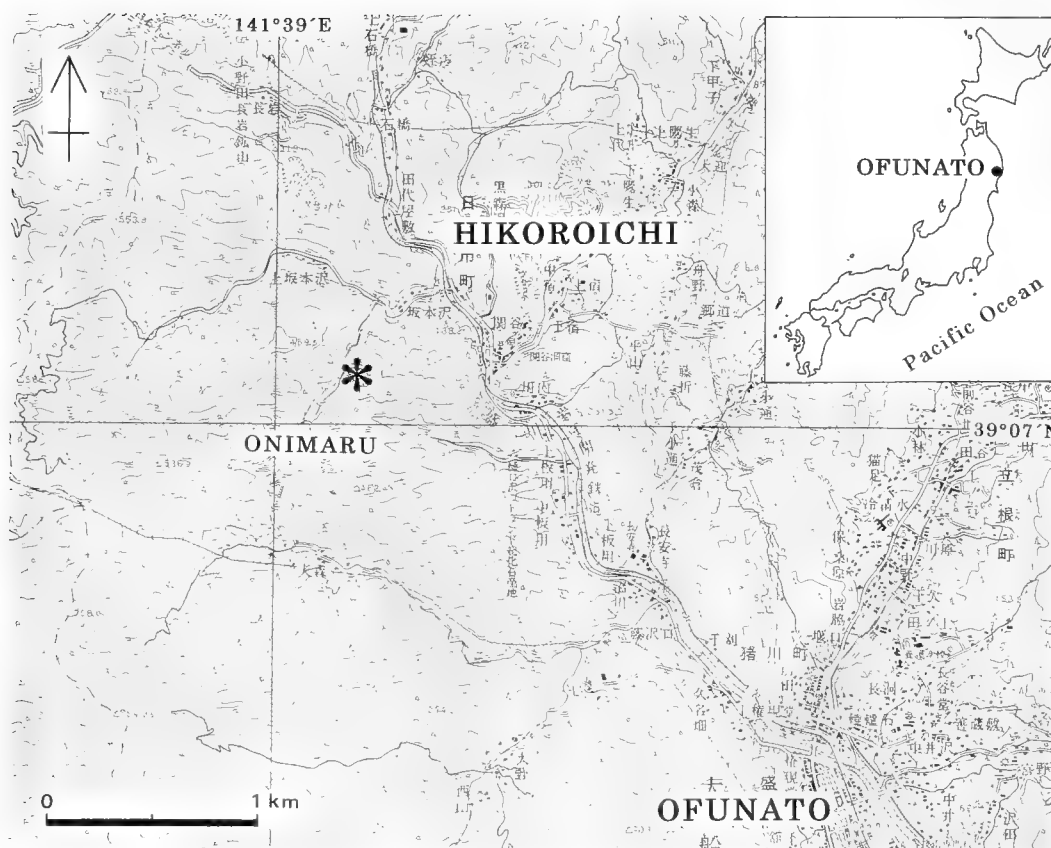
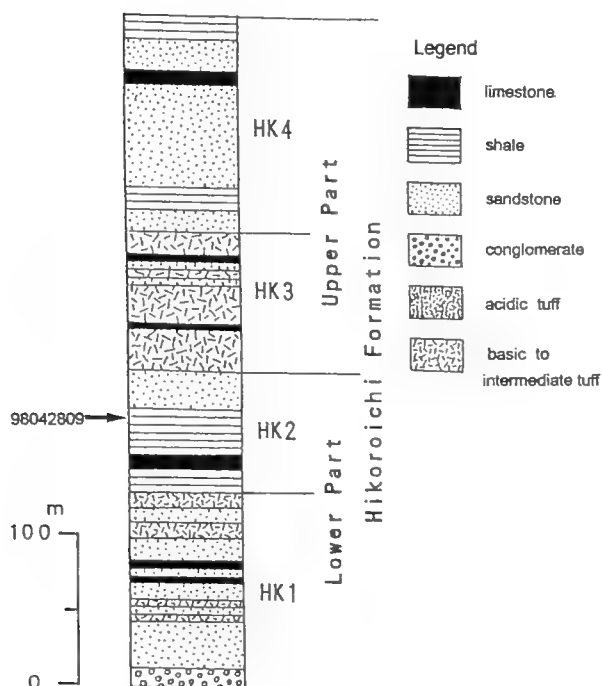


Figure 1. Index map showing the fossil locality (using the topographical map of "Sakari" scale 1:25,000 published by the Geographical Survey of Japan).



then demineralisation in dilute 35% HCL and 40% HF. Standard oxidation reagents did not react at all with the carbonized organic residues from the Hikoroichi Formation samples and so a very strong oxidation agent—fuming HN O_3 plus KCL ("fuming Schulze's solution") was used. The times required for oxidation using "fuming Schulze's solution" vary from sample to sample (as in Western Yunnan, Yang, 1993). In general, suitable oxidation will be achieved after seconds of oxidation. However, oxidation times for the Hikoroichi samples varied from one to several minutes even when heating the oxidation tube in a beaker of boiling water. Using this technique brown or light-brown coloured miospores were produced. Permanent slides were made with the rapid mounting medium Entellan.

Figure 2. Columnar section of the Hikoroichi Formation in the Hikoroichi area; arrow showing the stratigraphical horizon of the miospore fossils collected (adopted from Tazawa, 1984b).

Table 1. The paleontological data from the HK2 and HK3 Members of the Hikoroichi Formation in the Onimaru Quarry, Hikoroichi area, southern Kitakami Mountains, northeast Japan

| Taxonomic group | Literature source | Species |
|---|----------------------------|--|
| Lowermost part of the HK3 Member of the Hikoroichi Formation | | |
| Plant | Asama <i>et al.</i> (1989) | <i>Pseudosporochnus</i> n. sp., <i>Rhodeopteridium</i> sp. ?, <i>Sublepidodendron?</i> <i>wusihense</i> , <i>Lepidodendron</i> sp., <i>Archaeocalamites scrobiculatus</i> |
| HK2 Member of the Hikoroichi Formation | | |
| Coral | Kato <i>et al.</i> (1989) | <i>Amygdalophyllum</i> sp., <i>Bifossularia</i> sp., <i>Lophophyllidium</i> sp., <i>Multithecopora</i> sp., <i>Syringopora</i> sp. |
| Bryozoa | Sakaqami (1989) | <i>Acanthocladia?</i> sp. cf. <i>A. peculiaris</i> , <i>Hemitrypa?</i> sp. |
| Cephalopoda | Niko (1990) | <i>Adnatoceras onimarensis</i> , <i>Dolorthoceras</i> (?) sp., <i>Mooreoceras kinnoi</i> , <i>Neocycloceras</i> (?) sp., <i>Sueroceras nishimurai</i> . |
| Trilobite | Kaneko (1989) | <i>Linguaphillipsia choanjiensis</i> , <i>L. subconica</i> , <i>Liobole</i> (?) sp. |
| Gastropoda | Kase (1988) | <i>Baylea yvanii</i> , <i>Kawanamia onimarensis</i> , <i>Littorinides</i> sp., <i>Pseudozygopleura</i> (<i>Stephanozyga</i>) <i>nishimurai</i> , <i>Straparollus</i> (<i>Euomphalus</i>) <i>asanoi</i> , <i>S. (E.)</i> sp. |
| Brachiopoda | Tazawa (1989) | <i>Buxtonia</i> sp., <i>Lamellosathyris lamellosa</i> , <i>Linoprotonia</i> sp., <i>Marginatia</i> sp., <i>Unispirifer</i> sp. |
| Miospores | This paper | <i>Auroraspora</i> sp. cf. <i>A. macra</i> , <i>Calamospora</i> sp., <i>Crassispora trychera</i> , <i>Cyclogranisporites</i> sp., <i>Densosporites</i> sp., <i>Grandispora</i> sp. cf. <i>G. echinata</i> , <i>Leiotriletes</i> sp. cf. <i>L. incomptus</i> , <i>Microreticulatisporites araneum</i> , <i>Punctatisporites irrasus</i> , <i>P. minus</i> , <i>P. planus</i> , <i>Spelaeotriletes</i> sp. cf. <i>S. pretiosus</i> , <i>S. crustatus</i> , <i>Schophites</i> sp., <i>Verrucosisporites</i> sp. |

Palynostratigraphy

The miospore assemblages from the upper part of the lower Hikoroichi Formation (HK2 Member) in the Onimaru Quarry are relatively abundant compared with the Middle Permian ones from the Kanokura Formation in the Kamiyasse area, southern Kitakami Mountains, northeast Japan (Yang and Tazawa, 2000). Stratigraphically significant species include *Auroraspora* sp. cf. *A. macra*, *Crassispora trychera*, *Schopfites* sp., *Spelaeotriletes crustatus* and *S. sp.* cf. *S. pretiosus*. Common species are *Auroraspora* sp., *Calamospora* sp., *Crassispora* sp., *Cyclogranisporites* sp., *Densosporites* sp., *Grandispora* sp. cf. *G. echinata*, *Leiotriletes* sp. cf. *L. incomptus*, *Microreticulatisporites araneum*, *Punctatisporites minus*, *P. irrasus*, *P. planus* and *Verrucosisporites* sp.

Auroraspora macra is a common species in Lower Carboniferous (mainly Tournaisian) assemblages around the world (Van der Zwan and Walton, 1981). This species ranges from the latest Devonian (Famennian) to the earliest Viséan in Western Europe (Clayton *et al.*, 1977) and Australia (Playford, 1990). In Canada it ranges from the Tournaisian to early Viséan (Utting, 1987a, b). *Spelaeotriletes pretiosus* is mainly distributed from the Tournaisian to early Viséan in Poland (Turnau, 1978, 1979). Since it first appears in the late Tournaisian strata in Ireland, it was selected as an index

fossil for the PC (*Spelaeotriletes pretiosus*-*Raistrickia clavata*) Biozone by Higgs *et al.* (1988). However, it has occasionally been reported from the latest Devonian in Morocco (Rahmanin-Antari, 1990) and Eastern Alaska (Scott and Doher, 1967). *Spelaeotriletes crustatus* is commonly distributed from the late Famennian to late Tournaisian in SE Ireland (Higgs, 1975). *Crassispora trychera* is a characteristic species of the late Tournaisian to early Viséan in Western Europe (Clayton *et al.*, 1977), Poland (Turnau, 1978) and Canada (Utting, 1980; Utting *et al.*, 1989). It was once reported by Utting (1991) from the Lower Namurian in northern Yukon. *Schopfites* sp. is usually one of the common elements of the late Tournaisian and possible the early Viséan strata (Higgs *et al.*, 1988). The other species recorded include *Grandispora* sp. cf. *G. echinata*, *Leiotriletes* sp. cf. *L. incomptus*, *Densosporites* sp. and *Verrucosisporites* sp., which are also common members of the Early Carboniferous (mainly Tournaisian and Viséan) miospore assemblages from around the world.

Early Carboniferous (Tournaisian) miospore assemblages from Gengma, West Yunnan, China are correlated with the Western European BP and PC Biozones based on the occurrence of *Auroraspora macra*, *Kraeuselisporites hibernicus*, *Rugospora polyptycha*, *Spelaeotriletes balteatus* and *S. pretiosus* in the Longba Formation (Yang *et al.*, 1997).

All of the miospore taxa recorded from the Onimaru

| | | Western Europe Higgs <i>et al.</i> (1988) | Lower Yangtze Gao (1991) | S. Kitakami, Japan This paper | Nova Scotia Utting <i>et al.</i> (1989) |
|---------------|--------|---|--|--|--|
| Carboniferous | Viséan | Pu: <i>Lycospora pusilla</i> | Pu: <i>L. pusilla</i> | ? | No palynomorphs |
| | Tn3 | <i>Schopfites claviger</i> CM: <i>Auroraspora macra</i> | <i>S. claviger</i> CM: <i>A. macra</i> | <i>Schopfites</i> sp. <i>Crassispora trychera</i> <i>Auroraspora macra</i> | <i>C. decorus</i> - <i>S. claviger</i> <i>S.pretiosus</i> var. <i>pretiosus</i> |
| | | PC: <i>Spelaeotriletes pretiosus</i> <i>Schopfites claviger</i> | PB: <i>S.pretiosus</i> <i>Cingulizonates bialatus</i> | <i>Spelaeotriletes pretiosus</i> | <i>V. vallatus</i> |
| | Tn2 | BP <i>Spelaeotriletes balteatus</i> <i>Rugospora polyptycha</i> | ? | | Section faulted possibly incomplete |
| | | HD: <i>Kraeuselisporites hibernicus</i> <i>Umbonatisporites distinctus</i> | ? | | <i>E. rotatus</i> <i>H. explanatus</i> |
| | | VI: <i>Vallatisporites verrucosus</i> <i>Retusotriletes incohatus</i> | VI: <i>V. verrucosus</i> <i>R. incohatus</i> | | not studied |
| | Tn1 | LN: <i>Retispora lepidophyta</i> <i>Verrucosisporites nitidus</i> | LN: <i>R. lepidophyta</i> <i>V. nitidus</i> | | unconformity |
| Devonian | | | | | |

Figure 3. Suggested correlation of miospore assemblages from the southern Kitakami Mountains with late Devonian to early Carboniferous miospore biozones of Western Europe, Lower Yangtze and Nova Scotia.

Quarry are typical members of the latest Tournaisian (Tn3) in Western Europe (PB and CM Biozones), China (PC and CM equivalent Biozones), Nova Scotia and eastern Canada (*Spelaeotriletes pretiosus* var. *pretiosus* Biozone and *Crassispora trychera-Colatisporites decorus* Biozone). But most of them can extend to the early Viséan. A correlation chart of these biozones is provided in Figure 3.

The brachiopods (Tazawa, 1984a, 1985, 1989), gastropods (Kase, 1988) and cephalopods (Niko, 1990) from the HK2 Member of the Hikoroichi Formation at the Onimaru Quarry indicate an early Viséan age (see Table 1). However, the palynomorph assemblages from that member have a strong late Tournaisian character and are without the typical Viséan genus *Lycospora*. Furthermore, some plant fossils (*Archaeocalamites scrobiculatus*, *Knorria* sp. and *Sublepidodendron? wushiense*) were described by Asama *et al.* (1985, 1989) from the lowermost part of the H3 Member of Kawamura (1983), which is supposed to be equal to the HK3 Member of Tazawa (1985) at the same locality (see Table 1). *Archaeocalamites scrobiculatus* is one of the dominant representatives of Viséan plant assemblages in both South China and North China (Wu, 1995), and has also been reported by Wu (1995) from the Tournaisian of South China together with *Eolepidodendron wushiense* Sze or *Sublepidodendron? wushiense* Sze. It seems likely that the plant-bearing bed of the lowermost part of the HK3 Member is early Viséan. The Viséan *Lycospora pusilla* Biozone can be informally divided into a lower division containing rare *Lycospora pusilla* and an upper division with abundant representatives of that species (Higgs, 1996). This suggests that the miospore-containing strata of Onimaru Quarry can be dated as late Tournaisian to early Viséan rather than solely early Viséan as suggested by the brachiopods, gas-

tropods and cephalopods.

Sullivan (1965, 1967) first defined the differences between the various Early Carboniferous microfloral assemblages around the world and demonstrated a clear relationship between their distribution and their probable paleolatitude. He described five distinct assemblage suites in the Early Carboniferous, two (*Vallatisporites* Suite and *Lophozonotriletes* Suite) in the Tournaisian and three (*Grandispora* Suite, *Monilospora* Suite and Kazakhstan Suite) in the Upper Mississippian (late Viséan-early Namurian). In 1981, Van der Zwan supported Sullivan's conclusion through his statistically based correlation of late Tournaisian and early Viséan assemblages from 14 selected areas using both Jaccard and Simpson correlation coefficients. Clayton (1985) made some progress on microflora provinces proposing seven microfloras instead of Sullivan's five suites. In general, five microfloras can be distinguished in the Early Carboniferous (Clayton, 1985, figs. 2, 3) around the world: the *Granulatisporites frustulentus* Microflora in Australia, the *Spelaeotriletes balteatus* Microflora in North Africa, the Kazakhstan Microflora in Kazakhstan, and the *Vallatisporites* Microflora (middle Tournaisian to early Viséan) and the *Grandispora* Microflora (middle-late Viséan), which extended from the eastern United States and eastern Canada through Western Europe to China. The *Lophozonotriletes* Microflora (middle Tournaisian to early Viséan) and the *Monilospora* Microflora (middle-late Viséan) were mainly distributed in Western Canada, Spitsbergen and the north-western part of Russia. Assemblages from Eastern Europe are more or less transitional in nature between the *Vallatisporites* Microflora and the *Lophozonotriletes* Microflora.

The microflora in the southern Kitakami Mountains can be

circumscribed within the *Vallatisporites* Microflora in the sense of Clayton's division (Clayton, 1985) based on the presence of *Auroraspora* sp. cf. *A. macra*, *Crassisporea trychera*, *Spelaotriteles crustatus*, *S.* sp. cf. *S. pretiosus* and *Schopfites* sp.

Systematic palynology

The suprageneric classification used is mainly based upon the schemes by Potonié and Kremp (1954), Potonié (1956, 1975), Dettmann (1963) and Smith and Butterworth (1967).

Anteturma Sporites H. Potonié, 1893

Turma Triletes Reinsch emend. Dettmann, 1963

Suprasubturma Acavatitriteles Dettmann, 1963

Subturma Azonotriteles Lubert emend. Dettmann, 1963

Infraturma Laevigati (Bennie and Kidston) R. Potonié, 1956

Genus *Leiotriteles* (Naumova) Potonié and Kremp, 1954

Type species.—*Leiotriteles sphaerotriangulus* (Loose) Potonié and Kremp, 1954.

Leiotriteles sp. cf. *L. incomptus* (Felix and Burbridge)
Higgs, Clayton and Keegan, 1988

Figure 4.9

Compare.—

Punctatisporites incomptus Felix and Burbridge, 1967, p. 357, pl. 53, fig. 12.

Leiotriteles incomptus (Felix and Burbridge). Higgs *et al.*, 1988, p. 50, pl. 1, fig. 9.

Material.—Seven specimens logged from NU-P1 to NU-P4, Figure 4.9 from NU-P2.

Description.—Trilete acamerate miospores. Amb rounded triangular, sides convex. Suturæ simple and distinct, extending approximately to the equator. Laesurae bordered by flexuous labra. Exine laevigate, approximately 1.5–2 µm thick.

Diameter.—38–45 µm.

Remarks.—The Kitakami specimens are similar to those recorded by Felix and Burbridge (1967) as *Punctatisporites incomptus* and Higgs *et al.* (1988) as *Leiotriteles incomptus*, but are significantly smaller than the type (60–90 µm) and lack the prominent labra.

Genus *Punctatisporites* Ibrahim emend. Potonié and Kremp, 1954

Type species.—*Punctatisporites punctatus* (Ibrahim) Ibrahim, 1933.

Punctatisporites irrasus Hacquebard, 1957

Figure 4.7

Punctatisporites irrasus Hacquebard, 1957, p. 308, pl. 1, figs. 7, 8; Sullivan, 1964, p. 372, pl. 2, figs. 3.4; Higgs *et al.* 1988, p. 51, pl. 1, fig. 17.

Punctatisporites cf. *irrasus* Hacquebard. Dolby and Neves, 1970, p. 365, pl. 1, fig. 1.

Material.—Six specimens logged from NU-P2 to NU-P5, Figure 4.7 from NU-P2.

Description.—Acamerate trilete miospores. Amb subcircular. Suturæ distinct to obscure with a narrow labra. Suturæ extend 1/2 to 3/4 of the spore radius, usually darkening along its length. Exine 1–2 µm thick, often laevigate or finely infragranulate accompanying large compression folds.

Diameter.—45–54 µm.

Remarks.—The Kitakami specimens conform very closely to those described by Sullivan (1964), Dolby and Neves (1970), and Higgs *et al.* (1988), who reported size ranges of 59–98 µm, 42–65 µm and 50–92 µm, respectively.

Infraturma Apiculati Bennie and Kidston
emend. R. Potonié, 1956

Genus *Schopfites* Kosanke, 1950

Type species.—*Schopfites dimorphus* Kosanke, 1950.

Schopfites sp.

Figure 4.12

Material.—One specimen logged from NU-P4, distal view.

Description.—Miospore trilete, acamerate. Amb oval to circular. Suturæ distinct to indistinct, straight, extend almost to equator of miospores. Intexine thin, indistinct to distinct, approximately conformable with the amb, about 3/4 of the diameter. Distal surface and equator ornamented with pilae, rounded baculae, and rare verrucae. The size of the elements ranges from 0.5–3 µm in height and 0.5–2.5 µm in width. Sculptural elements are normally discrete and closely spaced. Proximal surface laevigate.

Diameter.—35 µm.

Remarks.—This specimen is attributed to the genus *Schopfites* on the basis of the type and distribution of the ornamentation, patchy distal ornament predominantly of verrucae, bacula or pila suggested by Higgs *et al.* (1988).

Genus *Verrucosisporites* Ibrahim emend. Smith, 1971

Type species.—*Verrucosisporites verrucosus* (Ibrahim) Ibrahim, 1933.

Verrucosisporites sp.

Figure 4.8

Material.—One specimen from NU-P2.

Description.—Trilete acamerate miospore. Amb rounded triangular. Suturæ distinct, simple, length 2/3 to 3/4 the spore radius. Exine 2–3 µm thick. Distal surface and equatorial region of proximal surface ornamented with verrucae. Verrucae 1.5–2.5 µm in basal diameter, 1.5–2 µm in height with predominantly rounded tops. Elements evenly spaced 3–5 µm apart.

Diameter.—40 µm.

Remarks.—This sole specimen from the southern Kitakami Mountains is unlike the previously described species of the genus *Verrucosisporites*.

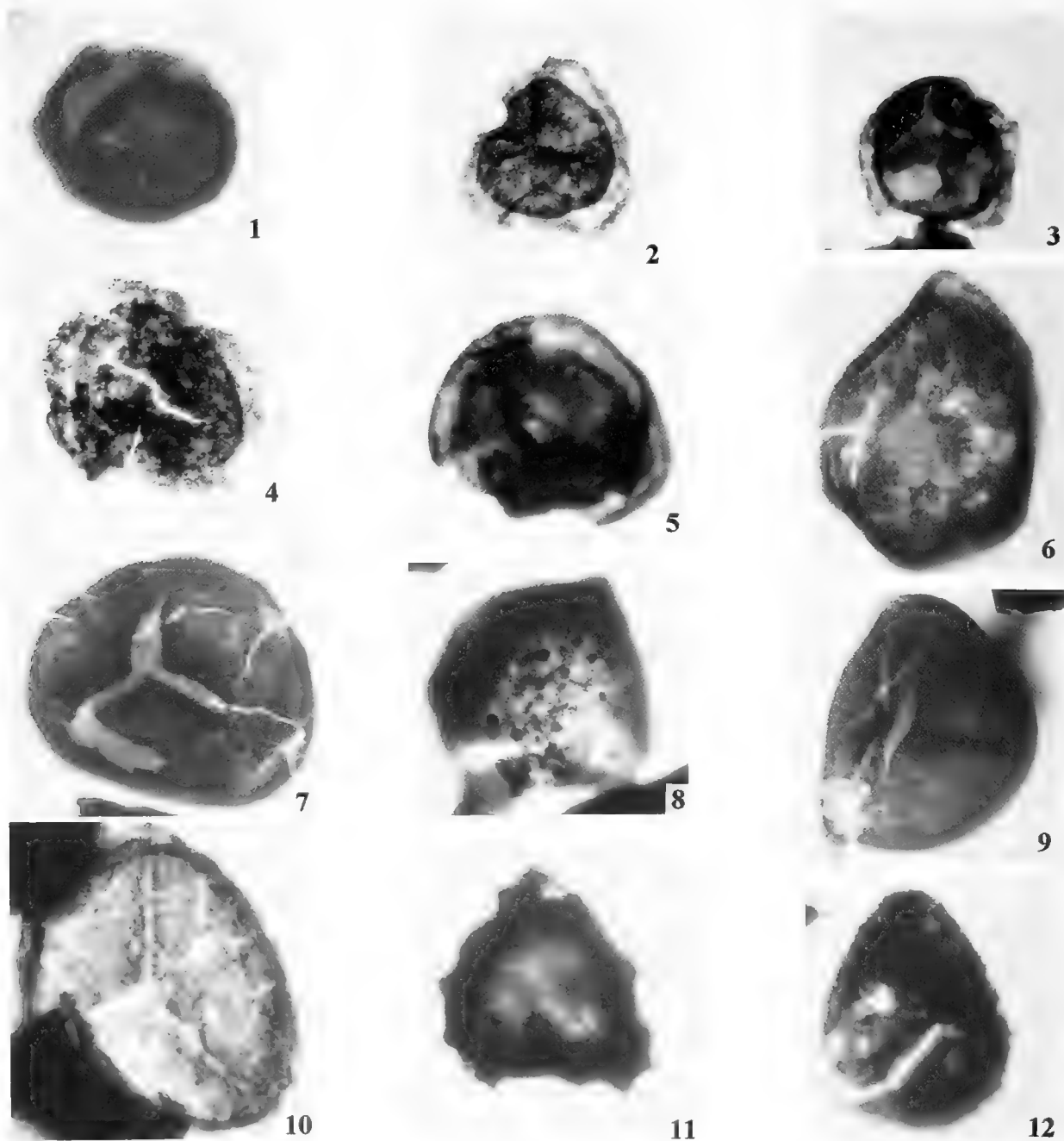


Figure 4. Early Carboniferous (late Tournaisian to early Viséan) miospores from the HK2 Member of the Hikoroichi Formation in the Onimaru Quarry, southern Kitakami Mountains, northeast Japan. The miospores are illustrated at the magnification of $\times 700$. **1.** *Microreticulatisporites araneum* Higgs, Clayton and Keegan, proximal view, high focus, NU-P5. **2, 3.** *Auroraspora* sp. cf. *A. macra* Sullivan. **2.** Proximal view, median focus, NU-P4. **3.** Proximal view, high focus, NU-P3. **4.** *Spelaeotriletes* sp. cf. *S. pretiosus* (Playford) Neves and Belt, proximal view, median focus, NU-P4. **5, 6.** *Spelaeotriletes crustatus* Higgs. **5.** Proximal view, high focus, NU-P5. **6.** Proximal view, median focus, NU-P3. **7.** *Punctatisporites irrasus* Hacquebard, proximal view, high focus, NU-P2. **8.** *Verrucosisporites* sp., distal view, median focus, NU-P2. **9.** *Leiotriletes* sp. cf. *L. incomptus* (Felix and Burbridge) Higgs, Clayton and Keegan, proximal view, median focus, NU-P2. **10.** *Crassispora trychera* Neves and Ioannides, proximal view, high focus, NU-P2. **11.** *Densosporites* sp., distal view, median focus, NU-P2. **12.** *Schopfites* sp., proximal view, median focus, NU-P4.

Infraturma Muornati Potonié and Kremp, 1954
Genus **Microreticulatisporites** Knox emend. Potonié
and Kremp, 1954

Type species.—*Microreticulatisporites lacunosus* (Ibrahim) Knox, 1950.

Microreticulatisporites araneum Higgs, Clayton
and Keegan, 1988

Figure 4.1

Dictyotrites sp. Keegan, 1977, p. 552, pl. 2, figs. 13–14.

Dictyotrites sp. B, Playford, 1978, p. 128, pl. 8, figs. 8–10.

Microreticulatisporites araneum Higgs, Clayton and Keegan, 1988,
p. 65, pl. 7, figs. 6, 9–10.

Material.—Six specimens logged from NU-P2, NU-P3, NU-P5, Figure 4.1 from NU-P5.

Description.—Trilete acamerate miospores. Amb subcircular to convexly triangular. Suturæ distinct to indistinct, straight to slightly sinuous and extending to the spore margin. Exine 1.5–2 µm thick, ornamented with close reticulum of tiny muri. Muri 0.5–1 µm in thickness, enclosing lumina 2–3 µm in width. Luminar usually polygonal to subcircular in shape. Reticulation normally comprehensive but occasionally less evident near equator and on the proximal surface.

Diameter.—30–35 µm.

Remarks.—These specimens, recorded from the southern Kitakami Mountains, are definitely attributed into *M. araneum* because of their particular reticulation and the size range.

Suprasubturma Laminatitrites Smith and Butterworth, 1967
Subturma Zonolaminatitrites Smith and Butterworth, 1967
Infraturma Crassiti

Genus **Crassispora** Bharadwaj emend. Sullivan, 1964

Type species.—*Crassispora kosankei* Potonié and Kremp emend. Bharadwaj, 1957.

Crassispora trychera Neves and Ioannides, 1974

Figure 4.10

Crassispora trychera Neves and Ioannides, 1974, p. 78, pl. 7, figs. 6–8; Higgs *et al.*, 1988, p. 55, pl. 3, fig. 24.

Material.—Four specimens logged from NU-P2 and NU-P3, Figure 4.10 from NU-P2.

Description.—Miospores trilete, variably camerate. Amb subcircular to rounded triangular. Suturæ straight, simple, extend almost to the margin of spores. The subparallel peripheral folding is often seen around the equator surface. Distal surface ornamented by the combination of coni, pila and grana (up to 1–1.5 µm in height).

Diameter.—53–68 µm.

Remarks.—These specimens are attributed to *C. trychera* by the presence of variable camerate and distal ornament of coni, pila and grana.

Suprasubturma Psedodsaccitritrites Richardson, 1965
Infraturma Monopseudosacciti Smith and Butterworth, 1967
Genus **Auroraspora** Hoffmeister, Staplin
and Malloy emend. Richardson, 1960

Type species.—*Auroraspora solisortus* Hoffmeister, Staplin and Malloy, 1955.

Auroraspora sp. cf. **A. macra** Sullivan, 1968

Figure 4.2, 4.3

Compare.—

Auroraspora macra Sullivan, 1968, p. 124, pl. 27, figs. 6–10; Higgs *et al.*, 1988, p. 69, pl. 9, figs. 17–19.

Material.—Ten specimens logged from NU-P1 to NU-P4, Figure 4.2 from NU-P4 and Figure 4.3 from NU-P3.

Diagnosis.—Size 48–68 µm, mean 58 µm (65 specimens); amb subcircular to irregular; exoexine laevigate, intexine laevigate to scabrate; trilete mark exceeds two-thirds radius of spore body

Description.—Trilete camerate miospores. Amb frequently irregular due to folding. Trilete straight, simple. Suturæ distinct with labra extend up to 2/3 or more of the spore radius. Exoexine thin, thickness not determinable, often finely folded in an irregular pattern, usually pitted and torn with fine grana. The equatorial darkened zone described by Higgs *et al.* (1988) is occasionally observed, Intexine 1.5 µm thick.

Diameter.—30–35 µm.

Remarks.—The specimens from the Hikoroichi Formation are similar to those described by Sullivan (1968) and Higgs *et al.* (1988) but are significantly smaller. Higgs *et al.* (1988) extend the size range of *A. macra* to 35–65 µm. The present specimens fall beyond this range and so are not attributed to *A. macra sensu stricto*.

Genus **Spelaeotrites** Neves and Owens, 1966

Type species.—*Spelaeotrites triangulus* Neves and Owens, 1966.

Spelaeotrites crustatus Higgs, 1975

Figure 4.5, 4.6

Spelaeotrites crustatus Higgs, 1975, pl. 6, figs. 7–9; non pl. 6, figs. 4–6.

Spelaeotrites exiguus Keegan, 1977, p. 556, pl. 4, figs. 7–10.

Spelaeotrites resolutus Higgs. Van der Zwan and Van Veen, 1978, pl. 2, fig. 1; Van der Zwan, 1980, pl. 18, fig. 5; Higgs *et al.*, 1988, pl. 13, figs. 8–9.

Material.—Seven specimens logged from NU-P3 to NU-P5, Figure 4.5 from NU-P5 and Figure 4.6 from NU-P3.

Description.—Trilete camerate miospores. Amb convexly triangular with rounded apices. Suturæ distinct, straight to slightly sinuous. Suturæ extend up to 3/4 of the spore radius, terminating in curvaturae perfectae. Exoexine 1–2 µm in thickness, distal surface and equator densely ornamented with fine to coarse grana and less commonly coni and small

spinae. Sculptural elements 1–1.5 μm in width, up to 1 μm in height, discrete but often fused to give short irregular-shaped rugulae. Intexine distinct to obscure, laevigate, almost conformable with amb, comprising 3/4 or more of the total spore diameter and attached to the exoexine on the proximal surface only.

Diameter.—50–60 μm .

Remarks.—These specimens recorded from the southern Kitakami Mountains are similar to *S. crustatus* with ornament mainly of fine to coarse grana instead of coni or small spinae usually distributed on the distal surface and equator.

***Spelaeotriletes* sp. cf. *S. pretiosus* (Playford) Neves and Belt, 1971**

Figure 4.4

Compare.—

Pustulatisporites pretiosus Playford, 1964, p. 19, pl. 4, figs. 9–7; pl. 5, fig. 1; text-fig. 1a.

Spelaeotriletes pretiosus (Playford). Neves and Belt, 1971, p. 1241; Higgs et al., 1988, pl. 13, figs. 16–18.

Material.—Six specimens logged from NU–P2, NU–P4, Figure 4.4 from NU–P4.

Description.—Trilete camerate miospores. Amb rounded to convexly triangular. Trilete distinct to indistinct, sinuous, suturae extend almost to the equator, terminating in curvaturae imperfectae. Exine infragranulate, 2 μm thick at the equator. Exoexine ornamented with low, simple verrucae, mammillate verrucae and wide-based spinae. Ornament evenly to irregular distributed, usually concentrated at the distal polar region and often discernible at the equator. Verrucae subcircular in basal outline, 2–3 μm in width, 1–2 μm in height, with rounded flattened or more commonly mammillate tops. Bases of verrucae discrete, or fused to form very large irregular-shaped verrucae.

Diameter.—35–38 μm .

Remarks.—The present specimens are assigned to *Spelaeotriletes* cf. *pretiosus* on the basis of the type of ornament. Playford (1964) indicated a size of 98 to 195 μm for the type material of *S. pretiosus*. Higgs et al. (1988) recorded specimens between 68 and 110 μm . The present specimens are considerably smaller.

Infraturma Cingulicamerati Neves and Owens, 1966

Genus ***Densosporites*** Berry emend. Butterworth, Jansonius, Smith and Staplin, 1964

Type species.—*Densosporites convensis* Berry in Butterworth, Jansonius, Smith and Staplin, 1963.

***Densosporites* sp.**

Figure 4.11

Densosporites sp. A, Higgs, Clayton and Keegan, 1988, p. 79, pl. 15, figs 10, 11.

Material.—Seven specimens logged from NU–P1 to NU–P4, Figure 4.11 from NU–P2.

Description.—Trilete cinguli-camerate miospores. Amb convexly triangular to subtriangular. Suturae obscure, simple, often gaping. Intexine often obscure. Exine 1–1.5 μm thick. Equatorial margin and distal surface ornamented with wide-based spinae, 1.5–2.5 μm in basal diameter and 1.5–3 μm in height. Spinae discrete but more commonly fused at their bases to form low sinuous and irregular cristae.

Diameter.—33–45 μm .

Remarks.—The Kitakami specimens are similar to those described by Higgs et al. (1988) in Ireland but just slightly smaller in size and with more dense ornament on the distal surface.

Conclusion

1. These records represent the first authenticated occurrence of Early Carboniferous miospores in Japan.
2. This significant miospore data might extend the geological age of the HK2 Member of the Hikoroichi Formation into late Tournaisian to early Viséan.
3. This miospore assemblage from the Hikoroichi area is more likely included in the *Vallatisporites* Microflora, which is to some degree similar to the Euramerican Realm in terms of megafloal phytogeography.

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***Pisulinella miocenica*, a new genus and species of Miocene Neritiliidae (Gastropoda: Neritopsina) from Eniwetok Atoll, Marshall Islands**

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Abstract. *Pisulinella* is proposed as a new monotypic genus in the neritopsine family Neritiliidae, with the single species *Pisulinella miocenica* sp. nov. This new taxon occurs in subsurface Miocene sediments from Eniwetok Atoll, Marshall Islands, western Pacific. Nine specimens of *P. miocenica* were previously regarded as close to *Nerita* (*Amphinerita*) *polita* Linnaeus of the Neritidae. Reallocation of this species from Neritidae to Neritiliidae is based mainly on the shape of the protoconch, which is conspicuously tilted relative to the teleoconch whorls and has several spiral ridges. The discovery of this neritiliid species, previously allocated to the Neritidae, suggests that detailed examination of protoconchs is necessary for defining the systematic position of fossil neritopsines. *Pisulinella miocenica* sp. nov. may have lived in a cryptic habitat.

Key words: Eniwetok, Neritiliidae, *Pisulinella miocenica*, protoconch, submarine cave

Introduction

The gastropod superorder Neritopsina has a fossil record from Silurian to Recent (Tracey *et al.*, 1993). This group underwent major adaptive radiation in the geological past, which has resulted in fairly diverse shell morphology and soft-part anatomy. The early history of neritopsine evolution is unknown, although some suprageneric phylogenies have been proposed for extant groups (e. g. Holthuis, 1995). Bandel (1992) documented the supposed earliest neritopsine from the Ordovician, although it differs greatly in teleoconch morphology from modern relatives. Unconventional species of neritopsines occur even in Recent faunas, such as the bizarre gastropod *Pluviosilla palauensis*, possibly belonging to a new neritopsine group, from a submarine cave in Palau (Kase and Kano, 1999). Additional discoveries such as these may eventually lead to a better understanding of neritopsine evolution.

Neritopsines are usually "neritiform" and tightly coiled, but may also have a limpet-like shape or, rarely, be shell-less (Cox and Knight, 1960; Ponder, 1998). Frequent convergence and parallelism, however, prevent reliable classification of the fossil forms and hinder an understanding of neritopsine evolution. Cox and Knight (1960) recognized

19 fossil genera of Neritidae and diagnosed most genera solely on the basis of general teleoconch shape. These fossil neritopsines must be reexamined to document their more conservative characters, such as shell microstructure, shell muscle scars, and protoconchs, in order to clarify their systematic positions. We describe a new genus and species in the family Neritiliidae from Miocene sediments at Eniwetok Atoll in the Marshall Islands, with special attention being given to protoconch morphology. This new species was once thought to be a modern species of the family Neritidae.

Materials

The nine specimens described here were recovered from three deep subsurface cores drilled by the U. S. Geological Survey in 1951–1952 on Eniwetok Atoll in the Marshall Islands. The drill holes penetrated Recent to upper Eocene sediments, and the cores and cuttings of the drill holes yielded gastropods of remarkably high diversity, which were described by Ladd (1966, 1972, 1977) in his series of monographs on Cenozoic polyplacophorans and gastropods of tropical western Pacific islands. Specimens of the present new species were recovered from cores at depths ranging

from 253 to 298 meters (830 to 978 feet) below the surface and dated as early to late Miocene. See Ladd and Schlanger (1960) and Schlanger (1963) for details of the drilling operations and stratigraphic information.

All specimens used in this study are in the National Museum of Natural History, Washington, D. C. (USNM). SEM examinations were made in a low vacuum mode without a metal coating.

Systematic paleontology

Superorder Neritopsina Cox and Knight, 1960

Family Neritiliidae Schepman, 1908

Genus *Pisulinella* gen. nov.

Type species.—*Pisulinella miocenica* sp. nov.

Diagnosis.—Genus similar to *Pisulina*. Inner lip of aperture smooth, convex, bearing three or four inconspicuous teeth at margin; a shallow groove on inner lip callus extends

along inner line. Outer lip thick, with a blunt, rounded margin and with weak tubercles along the interior. Protoconch multispiral, inclined; larval shell sculptured with six or seven spiral ridges.

Etymology.—Combination of the neritiliid genus *Pisulina* and *ellus* (Latin: diminutive), referring to the smaller shell similar to *Pisulina*.

Discussion.—Neritiliidae Schepman, 1908 is a distinct family in Neritopsina, but until quite recently it had been thought to be a subfamilial taxon (Neritiliinae) of Neritidae (e. g. Cox and Knight, 1960; Ponder, 1998). Based upon her extensive anatomical study, Holthuis (1995) has clarified the paraphyly of Neritidae, and shown that *Neritilia* (the type genus of Neritiliidae) is the first offshoot in the clade "Neritidae" + Phenacolepadidae. Recently, Kano and Kase (in press) have reallocated the submarine-cave genus *Pisulina* from Smaragdiinae in Neritidae to Neritiliidae, based on finding 11 synapomorphies of *Pisulina* and *Neritilia* in the anatomical and shell characters.

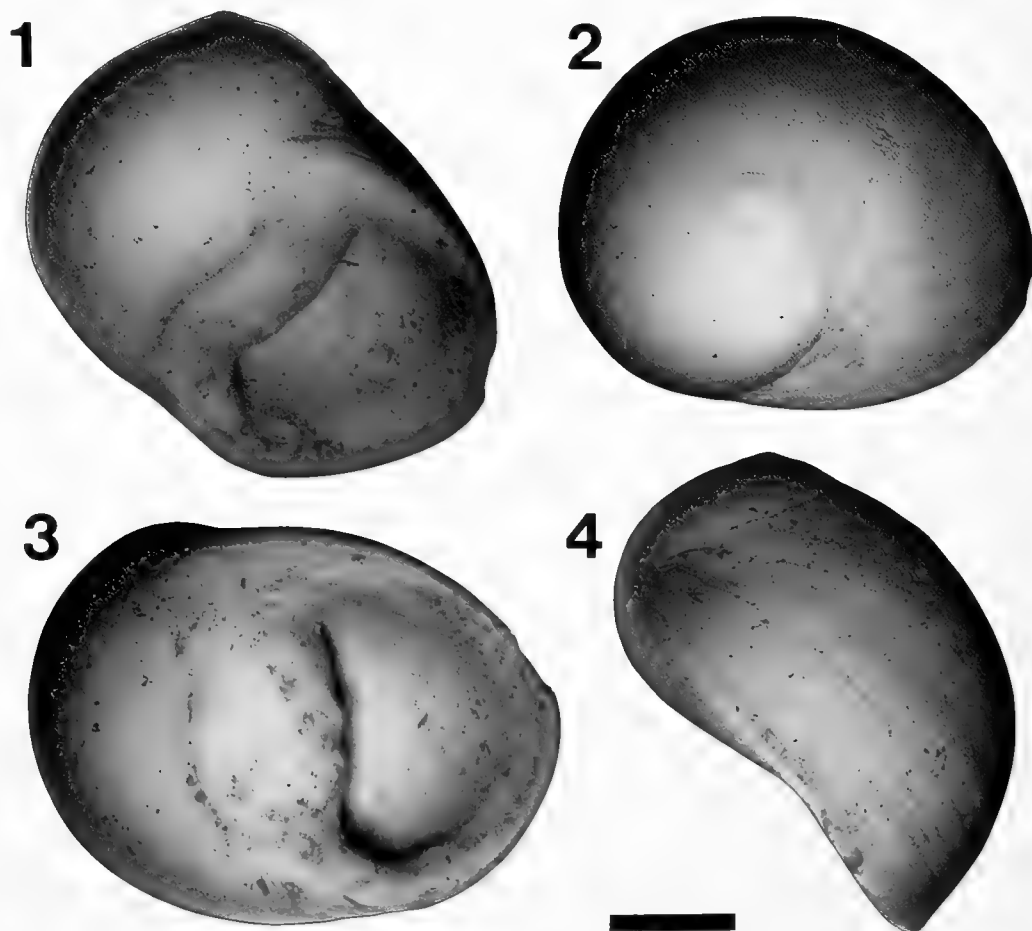


Figure 1. *Pisulinella miocenica* gen. et sp. nov. 1–4. Front, apical, apertural and lateral views of the holotype (USNM 648333). Scale bar = 1 mm.

The most important shell character for defining the taxonomic position of *Pisulinella* is protoconch morphology. The protoconchs of neritopsine species with planktotrophic development are unique and quite uniform in shape (e. g. Bandel, 1982). The larval shell is oval to globular-naticiform, smooth except for fine growth lines, and coils almost planispirally. Kano and Kase (in press) distinguish Neritiliidae from the other families in the superorder based on the fact that its coiling axis is remarkably tilted compared to that of the teleoconch, and because the protoconch surface bears several spiral ridges near the aperture. *Pisulinella* shares protoconch features with *Pisulina* and *Neritilia*, as described in the systematic part of this report. Although the soft anatomy of *P. miocenica* sp. nov. is not known, the new genus unequivocally belongs to Neritiliidae.

The family Neritiliidae heretofore included the two modern genera *Neritilia* Martens and *Pisulina* Nevill and Nevill (Kano and Kase, in press). *Pisulinella* is related to *Pisulina* rather than to *Neritilia*. *Neritilia rubida*, the type species of the genus, has a thin calcareous layer that covers the embryonic shell (Kano and Kase, in press). Bandel and Riedel (1998, fig. 6A, B) showed another example in a species of the genus from Cebu, Philippines, but the calcareous layer appears to be thinner than that of *N. rubida*. However, this layer is absent in *Pisulina* and *Pisulinella* (this condition in *Pisulina* is typically developed in *P. adamsiana*; see Herbert and Kilburn, 1991, fig. 3). Teleoconch morphology also indicates that *Pisulinella* is close to *Pisulina* rather than to *Neritilia*. In *Pisulinella* and *Pisulina* (particularly *P. adamsiana*), the inner line of the apertural inner lip callus has a reversed S-shape, and the basal lip bears a weak protuberance (Figures 1, 2). On the other hand, *Pisulinella*

possesses more numerous spiral ridges on the larval shell, and the exposed area of the embryonic shell is much smaller than in *Pisulina adamsiana*. The apertural morphology is also characteristic of *P. miocenica*. When the shell is fully grown, the outer lip is thickened along its interior with many obscure tubercles, and is blunt and rounded along its margin (Figure 2.1). Furthermore, the inner lip callus of *Pisulinella* has a shallow groove that extends along the inner line (Figure 2.2). None of the species of *Pisulina* and *Neritilia* have such features. We therefore conclude that *Pisulinella* is a distinct genus in Neritiliidae.

***Pisulinella miocenica* sp. nov.**

Figures 1–3

Nerita (*Amphinerita*) aff. *N. polita* Linnaeus: Ladd, 1966, p. 56, pl. 10, figs. 17, 18.

Diagnosis.—As for the genus.

Description.—Shell small, up to 4.0 mm in diameter, 3.7 mm in height (Table 1), thick, solid, obliquely ovate with a low spire, brownish cream in color without color markings (Figure 1). Inner walls of whorls resorbed, producing a hollow cavity inside. Protoconch multispiral, consisting of embryonic and larval shells, deeply immersed in first teleoconch whorl, separated from teleoconch by a clearly demarcated line; protoconch axis inclined significantly relative to teleoconch (Figure 3.1). Embryonic shell largely covered by larval shell and also sometimes by first teleoconch whorl, depending on protoconch inclination, and sculptured with faint, reticulate grooves (Figure 3.2); exposed portion of embryonic shell ca. 60 μ m in maximum dimension; larval

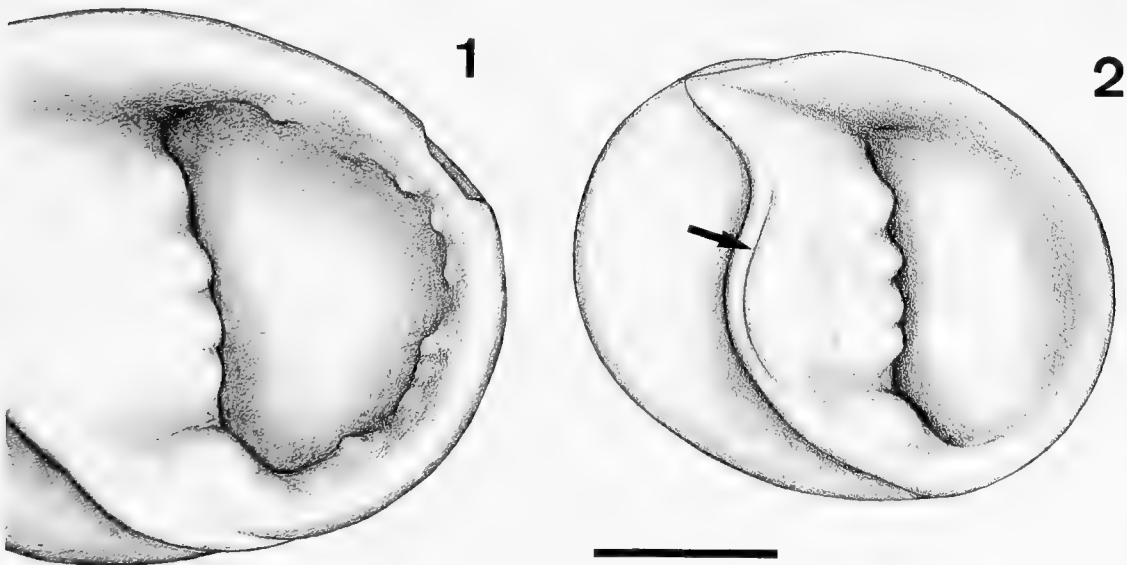


Figure 2. Drawings showing the detail of apertural characteristics in *Pisulinella miocenica* gen. et sp. nov. Scale bar = 1 mm. 1. Holotype with four teeth along the inner lip, a weak protuberance in the basal lip, and many obscure tubercles on the outer lip. 2. Paratype 6 (USNM), juvenile shell, with an unornamented outer lip that has a sharp margin. Arrow indicates a shallow groove in the inner lip callus along the inner line.

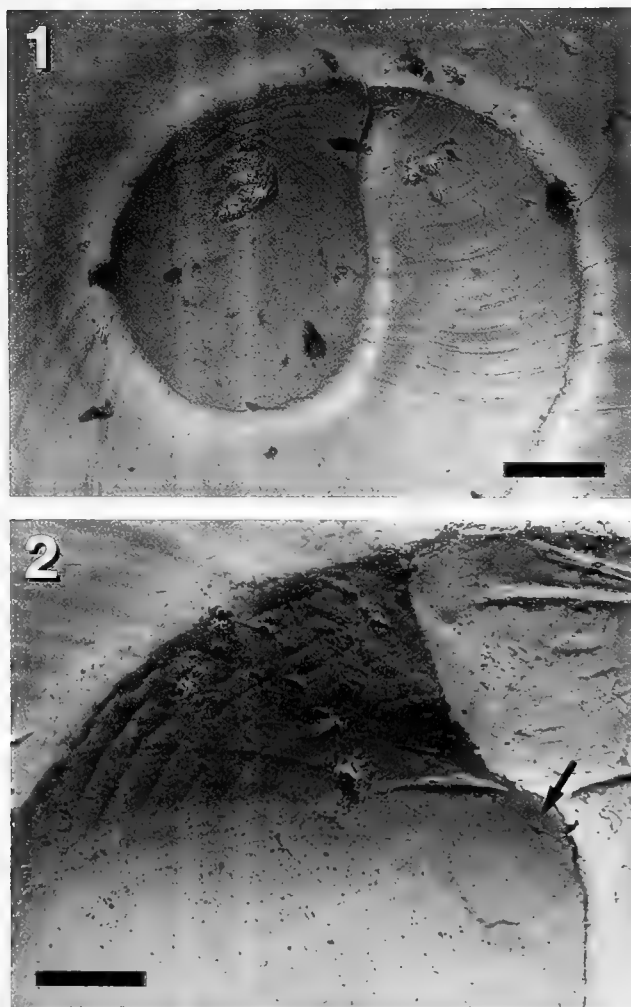


Figure 3. SEM micrographs of the protoconch of *Pisulinella miocenica* gen. et sp. nov. **1.** Apical area of paratype 8 (USNM). Scale bar = 100 µm. **2.** Protoconch of the holotype, showing an exposed embryonic shell (arrow) and seven spiral ridges on the larval shell. Scale bar = 50 µm.

Table 1. Locality and shell measurements of *Pisulinella miocenica* gen. et sp. nov. Paratypes 6–8 are immature specimens and have a sharp margin along their outer lips. The outer lips of paratypes 4 and 5 are largely broken so that the diameters and heights (in parentheses) are not representative of the species.

| Specimen | Hole number and depth (feet) | Number of teleoconch whorls | Diameter (mm) | Height | Maximum diameter of protoconch exposed (mm) |
|----------------------|------------------------------|-----------------------------|---------------|--------|---|
| Holotype USNM 648333 | F-1 (930–940) | 2.3 | 3.8 | 3.7 | 375 |
| Paratype 1 USNM | F-1 (920–930) | 2.3 | 4.0 | 3.4 | 325 |
| Paratype 2 USNM | F-1 or E-1 (940–950) | 2.2 | 3.7 | 3.3 | 335 |
| Paratype 3 USNM | F-1 (900–910) | 2.2 | 3.6 | 3.3 | 360 |
| Paratype 4 USNM | E-1 (830–840) | 2.2 | (2.7) | (2.9) | 365 |
| Paratype 5 USNM | F-1 (900–910) | 2.1 | (2.7) | (3.1) | 295 |
| Paratype 6 USNM | K-1B (968–978) | 2.0 | 3.0 | 2.7 | 385 |
| Paratype 7 USNM | K-1B (936–946) | 1.8 | 2.8 | 2.5 | 340 |
| Paratype 8 USNM | E-1 (900–910) | 1.6 | 2.0 | 1.9 | 365 |

shell surrounded by suture of first teleoconch whorl, and exposed drop-shaped area 295–375 µm in maximum dimensions, sculptured with microscopic pits scattered all over surface, and also with six or seven, ca. 3-µm-wide, up to 200-µm-long spiral ridges near apertural lip. Teleoconch whorls less than 2.3 in number, increase rapidly in size, inflated with a round periphery, slightly concave below sutures; last whorl more or less descending abapically in final growth stage. Suture shallowly impressed. Shell surface smooth, polished, and ornamented with fine growth lines and microscopic, sparse spiral grooves. Aperture widely open and semicircular in outline. Outer lip prosocline, blunt at margin, angled 30° to 40° to shell axis, and thickened along interior with many weak tubercles (Figure 2.1). Inner lip covered with a white, smooth, thick and convex callus; adaxial margin bears 3 or 4 slightly protruding teeth, inner line of callus with a deep and distinct, reverse-S shaped groove surrounding columellar area and continuing to basal lip without sinuation; a shallow groove carved on inner lip callus extends along inner line (Figure 2.2). Basal lip usually bears a weak protuberance. Operculum unknown.

Etymology.—The species name is derived from the word Miocene, the age of the specimens.

Types.—Holotype: USNM 648333, drill hole F-1 at depth of 930–940 feet (283–287 m), Elugelab Island, Eniwetok Atoll, Marshall Islands, lower Miocene (Tertiary *f*). Eight paratypes, USNM, from three drill holes F-1, K-1B, E-1 (on Elugelab Island, Engebi Island, and Parry Island, respectively), Eniwetok Atoll, at a depth of 830–978 feet (253–298 m), lower to upper Miocene (Tertiary *f–g*). See Table 1 for details.

Occurrence.—This species is known only from drill-holes on Eniwetok Atoll, early to late Miocene.

Discussion.—Ladd (1966) assigned this species to *Nerita* (*Amphinerita*) in Neritidae and suggested an affinity to *N. (A.) polita* Linnaeus, a modern species widely inhabiting the tropical Indo-West Pacific, including the Marshall Islands. However, the present fossil species differs markedly from *N. (A.) polita* and also from other species of the subgenus in several important ways. The fully grown adult shell of *P. miocenica* is less than 4 mm in maximum diameter (Table

1), while the largest specimen of *N. (A.) polita* at hand, from Okinawa, Japan, is over 35 mm in maximum diameter. Even the smallest adult of *Nerita (Amphinerita)* species at hand is over 15 mm in maximum diameter. Moreover, the shells of *P. miocenica* are plain cream in color and lack the color pattern that is characteristic of *Nerita (Amphinerita)*. Ladd (1966, p. 11) stated that the fossil shells in the drill-hole section from which this species was recovered apparently never were raised above sea level to be leached and recrystallized. The shells of this new species are almost intact, and many mollusk shells from the same section retain original color patterns (e. g. *Smaragdia* species; see Ladd, 1966, pl. 11, figs. 5–9). These facts strongly suggest that shells of *P. miocenica* were originally plain white, but were subsequently stained brownish cream during fossilization. The presence of a distinct inner line in the callused apertural inner lip, also noted by Ladd (1966), is another character separating *P. miocenica* from *Nerita (Amphinerita)* species.

Schlanger (1963) stated that the reef-associated sediments in the drill-hole section from which the shells of *P. miocenica* were recovered were deposited in lagoonal and shore-bank environments. The basis for this belief was the very high content of delicate branching corals and the abundance of large mollusks. Gastropod species associated with *P. miocenica* in the drill holes include a number of microscopic and macroscopic species that also are suggestive of lagoonal and shore-bank environments within a coral reef. Interestingly, however, the plain creamy color of *P. miocenica* suggests a cryptic habitat for this species. Loss of shell color and reduction of shell size are adaptations to gloomy to totally dark cave habitats for mollusks (Kase and Hayami, 1992; Hayami and Kase, 1993, 1996). Four *Pisulina* species found in marine caves are plain white in color and lack color markings (Kano and Kase, in press). Seven species of undescribed neritiliid genera recently found in submarine caves of tropical Pacific islands, and a species of *Neritilia* recently found in anchialine caves (subterranean caves with haline water which have no surface connection to the sea; see Stock *et al.*, 1986), are entirely white (unpublished data). We suggest that *P. miocenica* was a cryptic species that inhabited submarine caves and/or crevices in a coral reef, and that the shells were secondarily transported to an open reef-associated environment by water currents and/or by subsequent destruction of the reef bodies.

Acknowledgements

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A new fossil bonito (Sardini, Teleostei) from the Eocene of England and the Caucasus, and evolution of tail region characters of its Recent relatives

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Abstract. A new species of a fossil bonito, *Gymnosarda prisca* (Scombridae, Perciformes) from the Early Tertiary shows an interesting combination of characters not seen in other, Recent, bonitos. The new species is based on hypural bones from the caudal region. Although a bonito, the fossil hypural plates possess a caudal notch, a character not known in Recent bonitos. The discovery of this new taxon causes a redefinition of the synapomorphies of the caudal region that define bonitos and their relatives, the tunas and Spanish mackerels. The fossil species has previously been described as part of *Scomberomorus saevus*.

Key words: bonitos, evolution, fossil, new species, synapomorphies, tunas

Introduction

The discovery of a new fossil fish has changed concepts of the characters that define tunas, bonitos and the evolution of their characters. Tunas and bonitos (tribes Thunnini and Sardini, Scombridae) have been stably defined for sometime according to characteristics described in Collette and Chao (1975), Collette (1978) and Collette *et al.* (1984). A new fossil scombrid, described here, shows a remarkable combination of characters which changes current concepts. This fossil species has been studied in the context of a phylogenetic study of the suborder Scombroidei. The main hypotheses (Collette *et al.*, 1984; Johnson, 1986; Finnerty and Block, 1995) on phylogenetic relationships of scombroid fishes, based on data of Recent taxa, present highly conflicting results. In an attempt to solve this problem, I carry out a phylogenetic analysis, containing Recent as well as fossil taxa. Here I present part of my results.

Scomberomorus saevus Bannikov was described from the Eocene of Turkmenistan and Kazakhstan (Bannikov, 1982, 1985). This paper concerns amongst others a specimen of a hypural plate, originally assigned to *S. saevus*. Hypural elements are bones that provide the principal support for the lepidotrichia of the tail in fishes, and are normally separate from one another. In the Scombridae the hypural elements are fused to such a degree that they form one single hypural plate. This plate articulates directly with the vertebral column. Bannikov (1982) did not describe hypural plates in the original description of *S. saevus*, although the type material did include these plates (Bannikov pers. comm., 1998).

They are described in a later account (Bannikov, 1985). These hypural elements are part of a series of paratypes. The holotype of *S. saevus* is a premaxilla. Bannikov's (1982, 1985) material of *S. saevus* includes one specimen which I have identified as Sardini. One fossil specimen from England has been identified as identical to the aforementioned Sardini.

Materials

Except for RAN PIN 1878-8 (premaxilla), the fossil material consists of hypural plates.

BMNH: the Natural History Museum, London:

New species: P6485, Isle of Sheppey, England, Ypresian (London Clay Formation).

Gymnosarda unicolor (Rüppell): 1934.3.31, Red Sea (Recent).

Scomberomorus niphonius (Cuvier): 1874.1.16.9, no data; 1890.2.26.90, inland sea, Japan (Recent).

Sarda orientalis (Temminck and Schlegel): 1920.7.23.59, Durban, South Africa (Recent).

RAN PIN: Russian Academy of Sciences, Paleontological Institute, Moscow:

New species: 1878-2 Western extremities of Ustyurt, Kazakhstan, Upper Eocene (Shorym Svita); 1878-4, Turkmenistan, Upper Eocene (Shorym Svita); 1878-8 (holotype of *S. saevus*), Mangyshlak Peninsula, Karagiye basin, Kazakhstan, Upper Eocene (Shorym Svita).

USNM: Natural History Museum, Smithsonian Institution, Washington DC:

Scomberomorus plurilineatus (Fourmanoir): 64809 and 269760, Durban, South Africa (Recent).

Sarda sarda (Bloch): USNM 26953, 26954, no data (Recent); 270730, New Jersey, U.S.A. (Recent); 270731, Ponte Delgada Fish Market, San Miguel, Azores (Recent).

Systematic palaeontology

Order Perciformes sensu Johnson and Patterson, 1993

Suborder Scombroidei sensu Carpenter *et al.*, 1995

Family Scombridae Rafinesque, 1815

Genus *Gymnosarda* Gill, 1862

Gymnosarda prisca sp. nov.

Figure 1A, B

Scomberomorus saevus Bannikov, 1982, p. 135 (in part); Bannikov 1985, p. 37 (in part).

Holotype.—BMNH P6485, (previously labelled “unidenti-

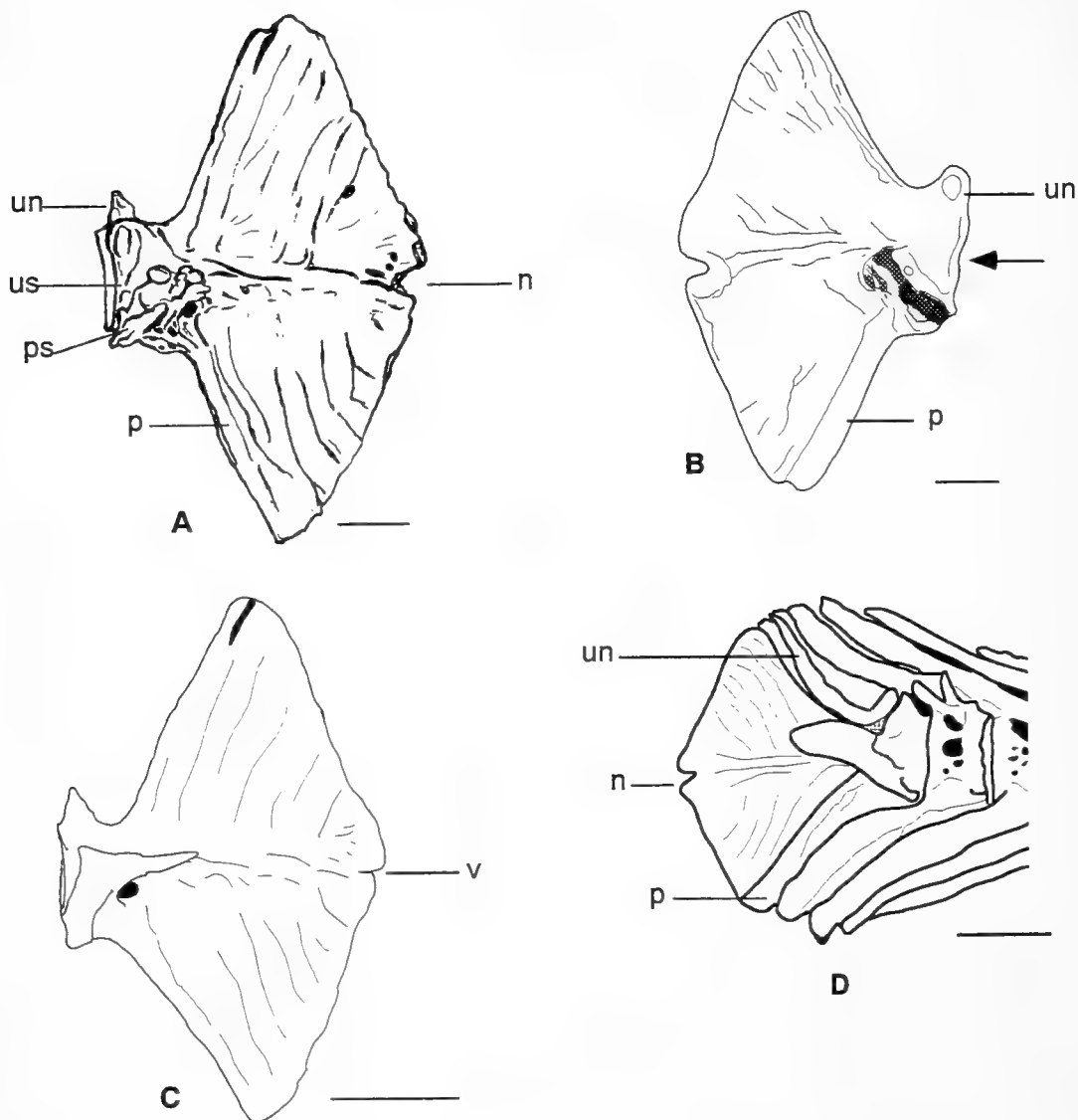


Figure 1. Hypural plates, lateral view. *Gymnosarda prisca* sp. nov. **A.** Holotype, BMNH P6485 (left view). **B.** RAN PIN 1878-4 (right view). Arrow indicates perspective of Figure 2A. **C.** *Gymnosarda unicolor* (Rüppell) (left view), after Collette and Russo (1984) and BMNH 1934.3.31. **D.** *Scomberomorus regalis* (Bloch): USNM 270053, (right view). Abbreviations: hyp5: fifth hypural, n: caudal notch, p: parhypural, ps: parhypurapophysis, un: uroneural, us: urostyle, v: remnant of caudal notch. Scale bars indicate 10 mm.

fied teleost") (Figure 1A).

Material.—Holotype, and RAN PIN 1878-4, (Figure 1B).

Etymology.—*Priscus* is Latin for "old", indicating it is an extinct ancient species of *Gymnosarda*. The only other species is the Recent *Gymnosarda unicolor*.

Diagnosis.—Species of a Sardini: uroneural and fifth hypural fused to hypural plate and urostyle cross-section with long axis horizontal. Differs from other Sardini by having parhypural fused to hypural plate and possession of caudal notch. Recent bonitos lack a conspicuous notch, and of Recent bonitos only *Gymnosarda unicolor* has a fused parhypural (see Figure 1).

Description.—Hypural plate, made up of fusion of urostyle, uroneural, hypurals 1-5 (hypural 5 not completely fused to plate) and parhypural. Plate diamond-shaped; sides equal in length. Height 75 mm (holotype, Figure 1A) or 79 mm (RAN PIN 1878-4, Figure 1B), which is twice the length without uroneural in both specimens (length: along axis of fish, height: along line perpendicular to axis). Posterior outline of diamond slightly swollen outwardly (more on dorsal side). Posteriorly, a clearly discernible notch. Markings made by fin rays crossing plate visible as shallow grooves, running parallel to rostral sides of diamond. Parhypurapophysis (damaged) making angle of about 41° with horizontal axis. Uroneural large, fused to urostyle [urostyle, according to definition of Potthoff (1975): fusion of preural centrum 1 and ural centrum]. Cross-section of urostyle round or slightly ovoid with the long axis vertical (as Thunnini, Figure 2).

Remarks.—The hypural plate-based taxon *G. prisca* is referable to the Sardini based on the diamond-shaped plate and the large anterior upturned end of the uroneural which is fused to the plate. With its proportions the hypural plate of *G. prisca* is almost identical to that of the Recent *G. unicolor* (Figure 1C). In *Gymnosarda*, the hypural plate is about twice as deep as long. In the other bonitos *Sarda*, *Orcynopsis* and *Cybiosarda* the hypural plate is less deep. *Allothunnus* was previously recognised as a bonito (Collette and Chao, 1975; Johnson, 1986). Collette *et al.* (1984) suggest that *Allothunnus* is better regarded as a primitive Thunnini, for which later convincing evidence has been found (Graham and Dickson, in press). *Gymnosarda unicolor* is unique among Recent bonitos in having a fused parhypural, just like *G. prisca*, and has a small vestige where *G. prisca* has a caudal notch (BMNH 1934.3.31 and Collette and Chao, 1975, p. 578 and fig. 56). No bonito with a caudal notch is known (Collette and Chao, 1975). I have not seen such notches in specimens of *Sarda* (BMNH 1920.7.23.59; USNM 26953, 26954, 270730 and 270731). Still, the *G. prisca* hypural plate possesses all other characteristics of a Sardini.

The specimen figured in Figure 2B (RAN PIN 1878-2) is an unknown scombrid, described and figured as *S. saevus* by Bannikov (1985, p. 37, figures 17 g, d) and is part of the *S. saevus* type series. The parhypural is fused to the plate and hence it is not a *Scomberomorus* (Table 1; see also Discussion), but no name as yet is assigned to that specimen. The systematic position of the taxon this plate represents is still under consideration.

Discussion

Previously, *G. prisca* was believed to belong to *Scomberomorus* because of apparent similarities with the latter (Figure 1D). It now seems that it is not a *Scomberomorus*. The most conspicuous character to identify a Sardini from a Scomberomorini is the cross-section of their urostyles (see their descriptions and Figure 2). *Gymnosarda prisca* has a hypural plate in which the cross-section of the urostyle is ovoid with the long axis vertical (Figure 2A), whereas in Scomberomorini the long axis is horizontal (Figure 2B). In *G. prisca* the parhypural is fused with the hypural plate, whereas in Recent *Scomberomorus* it is not. Collette and Russo (1984) mention that *Scomberomorus niphonius* and *Scomberomorus plurilineatus* have parhypurals partially fused to the hypural plate. In specimens of *S. plurilineatus* (USNM 264809 and 269760) and *Scomberomorus niphonius* (BMNH 1874.1.16.9 and 1890.2.26.90) the parhypural is not fused to the hypural plate. Possibly there is a light degree of fusion in specimens that I have not seen. Bannikov (1982) noted that the parhypural of *S. saevus* is separated from the hypural plate by a fissure. Although the parhypural can be clearly identified in the hypural plate of *G. prisca*, the division between the plate and the parhypural is not sharp enough to represent an autogenous parhypural.

The assignment of the name *S. saevus* to its whole type series is partially incorrect. Bannikov's (1982, 1985) holotype is RAN PIN 1878-8, which is a premaxilla that is identical to one of *Scomberomorus*. A *Scomberomorus* premax-

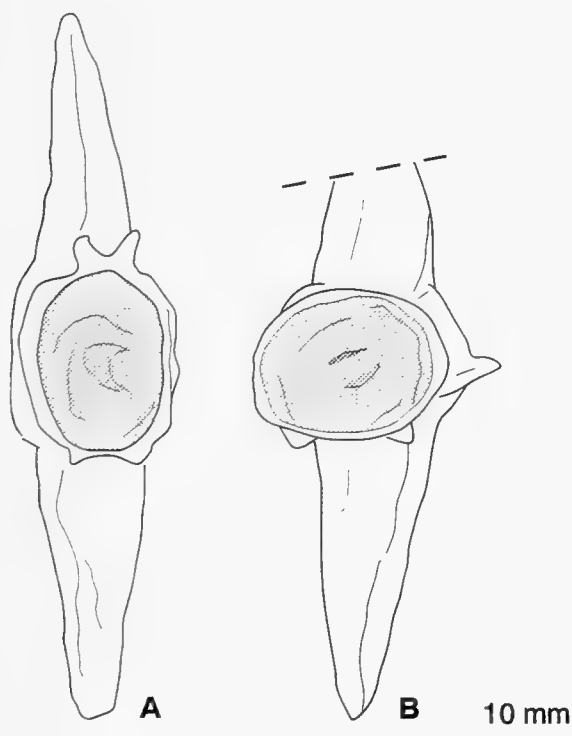


Figure 2. Hypural plates viewed to show the diameters of urostyles. **A.** *Gymnosarda prisca* sp. nov., RAN PIN 1878-4. **B.** *Scomberomorini* indet., RAN PIN 1878-2.

illa is recognised by a relatively long ascending process: 31–48% of the total premaxilla (Collette and Russo, 1984), and makes a sharp angle with the shank: 32°–61° (Collette and Russo, 1984). The holotype of *S. saevus* fits this description well. Being recognised as a *Scomberomorus* and being the holotype of the epithet *saevus*, the name *Scomberomorus saevus* is retained for this specimen.

Gymnosarda prisca shows a peculiar mix of characters. A noticeable caudal notch in the hypural plate is a primitive character, found in amongst others the Scomberomorini, where it can be large. I do not think that *G. prisca* can be anything but a Sardini and indeed, a *Gymnosarda*. According to Collette and Chao (1975) and Collette *et al.* (1984)

one of the synapomorphies of the scombrids above the Spanish mackerels (Scomberomorini) is the absence of the caudal notch (see Table 1). *Gymnosarda prisca* clearly possesses a large caudal notch. *Gymnosarda unicolor* is in fact not devoid of a caudal notch, it has a small, hard to spot vestigial one. It seems thus, that Sardini are not characterised by the absence of a caudal notch, but rather by a tendency of this notch to close down, and ultimately disappear in their evolution. Thunnini are characterised by a complete absence of the notch. The caudal notch in *G. prisca* is evidence that it is not a sharp divider above species level: the Scomberomorini have a notch; so do primitive Sardini and in advanced ones this notch has disappeared. Therefore, be-

Table 1. Overview of hypural plate characters of *Scomberomorus* and Sardini.

| | Parhypural | Caudal notch | Uroneural | Hypural fusion pattern | Cross-section of urostyle |
|--------------------------------------|------------|--------------|-----------|------------------------|---------------------------|
| <i>Scomberomorus</i> | not fused | yes | not fused | 1–4, 5 | long axis vertical |
| <i>Gymnosarda prisca</i> sp. nov. | fused | yes | fused | 1–5 | long axis horizontal |
| <i>Gymnosarda unicolor</i> (Rüppell) | fused | remnant | fused | 1–5 | long axis horizontal |
| other Sardini | not fused | no | fused | 1–5 | long axis horizontal |

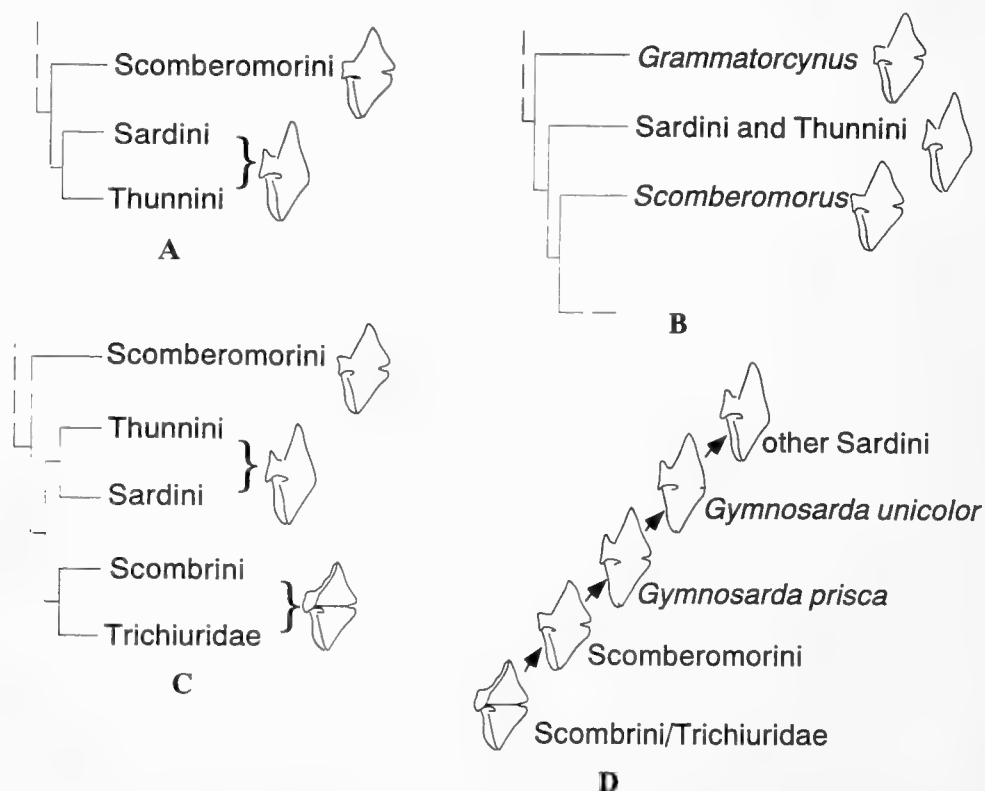


Figure 3. Phylogenetic relationships of Sardini, Thunnini and their closest relatives. **A.** After Collette *et al.* (1984). **B.** After Johnson (1986). **C.** After Finnerty and Block (1995). **D.** Proposed evolutionary sequence.

cause of the great similarities with *G. unicolor*, I describe this fossil taxon as a new species within this genus.

The small vestigial notch of *G. unicolor* suggests that more primitive bonitos have once had a large caudal notch. This is confirmed by *G. prisca*. This notch is a primitive feature, which thus suggests that the ancestor of the bonitos came from within the Scomberomorini (see Table 1).

Collette *et al.* (1984) and Johnson (1986) published phylogenies of Scombroidei based on morphological data (Figs. 3A and B). Finnerty and Block (1995) published a phylogeny based on DNA analyses (Figure 3C). In Collette *et al.* (1984), Sardini and Thunnini are the most advanced scombroids, with Scomberomorini as the sistergroup. According to Johnson (1986), Sardini+Thunnini are a specialised offshoot of a paraphyletic Scomberomorini. Finnerty and Block (1995) present a phylogenetic relationship in which the Sardini+Thunnini clade is sister-group to a Scombrini (mackerels)+Trichiuridae (cutlassfishes) clade. The clade containing these four taxa is in turn the advanced sistergroup to Scomberomorini. Keeping in mind the proposed evolutionary sequence (Figure 3D), all three hypotheses of relationships in Fig. 3A–C seem to be possible. Finnerty and Block's hypothesis is less parsimonious than the morphological ones, because it requires reversals. The caudal region of Scombrini and Trichiuridae is plesiomorphic compared to that of other Scombridae. Johnson's (1986) Scomberomorini are paraphyletic, caused by the offshoot of Sardini and Thunnini, but his phylogenetic hypothesis remains possible. However, this hypothesis is less parsimonious than that of Collette *et al.* (1984). If you map tail-region morphology on Johnson's (1986) phylogeny, there are character reversals (Figure 3B). Further research on the phylogeny of scombroids will hopefully contribute more to the solution of the controversy of these relationships.

Although based on a hypural plate only, I do think that phylogenetic hypotheses can be made using *G. prisca*. Hypural plates provide strong characters, which are well indicative of genera (see Uyeno and Fujii, 1975).

Conclusions

While studying the type series of *Scomberomorus saevus*, a new species has been found: *Gymnosarda prisca*. Sardini are to be characterised by a tendency of the hypural notch to close and disappear in their evolution. Thunnini are characterised by a complete absence of the notch. *Gymnosarda prisca* fits in with every one of the different scombroid cladograms, with respect to Recent Sardini-Scomberomorini relationships. Finnerty and Block's (1985) phylogeny seems to be less parsimonious than the morphological phylogenies. In Johnson's (1986) hypothesis, Scomberomorini are paraphyletic and the tail region evolution requires reversals.

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◎第149回例会は、2000年6月24日（土）と25日（日）に「群馬県立自然史博物館」で開催されます。個人講演の申し込み締切日は2000年5月2日（火）です。6月24日（土）にシンポジウムとして「1500万年前頃の群馬の海—そのおいたちと生物たち—世話人 長谷川善和・高桑祐司・間嶋隆一」が開催されます。なお、このシンポジウムは富岡市民向けの公開講座もかねております。

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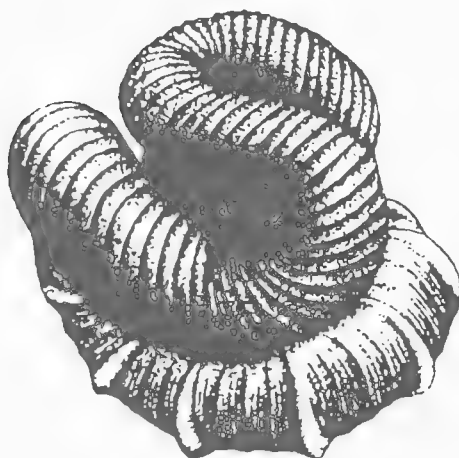
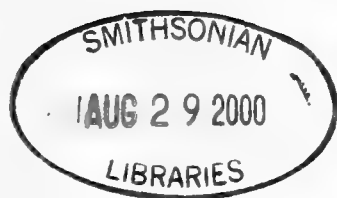
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Cover: Idealized sketch of *Nipponites mirabilis* Yabe, a Late Cretaceous (Turonian) nautiloid ammonite. Various reconstructions of the mode of life of this species have been proposed, because of its curiously meandering shell form (after T. Okamoto, 1988).

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Orthoconic cephalopods from the Lower Permian Atahoc Formation in East Timor

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Abstract. Three species of orthoconic cephalopods, *Mooreoceras* sp. and *Atahoceras timorensis* gen. and sp. nov. of the Pseudorthoceratidae, and an indeterminate genus and species of the Bactritidae are described from the Lower Permian Atahoc Formation in the Cribas area, East Timor. Apparent changes in the surface ornamentation of *Atahoceras* are considered to be genus-level criteria that separate it from the most closely related genus, *Bitauinoceras*. This assemblage signifies a non-ammonoid cephalopod fauna in the northern margin of Gondwana near the Sakmarian/Artinskian boundary.

Key words: *Atahoceras* gen. nov., Bactritida, East Timor, Gondwana, Orthocerida, Sakmarian/Artinskian boundary

Introduction

Timor is the largest (maximum ca. 365 km long and 100 km wide) island in the Banda Arc of the Indonesian Archipelago, where corresponds to a collision zone between the Indo-Australian and Asian Plates. Thus, the geology of this island is structurally complex. Carter *et al.* (1976) stated that the older rocks on Timor consist of the autochthonous Australian facies and overthrusting units derived from the Asian island arc. The purpose of this study is to document and describe an Early Permian orthocerid and bactritid cephalopod fauna of the Atahoc Formation, which is part of the autochthonous facies. The materials were collected by one of us (K. N.) from the right bank of the River Sumasse, west of Cribas under cooperation with H. Suzuki and T. Takahashi during field work of 1961 in East Timor (Figure 1). Other than "Orthocéres" that were reported by Gageonnet and Lemoine (1958), this is the first description of non-ammonoid cephalopods from the Atahoc Formation.

The Lower Permian Atahoc Formation is made up of the oldest exposed sediments in East Timor, and forms the Cribas Anticline together with the Upper? Permian Cribas, the Triassic Aitutu and the Triassic to Jurassic Wai Luli Formations in the Cribas area (Audley-Charles, 1968; Figure 1). It consists of more than 600 m of sandstone and shale with thin intercalated beds of limestone and basaltic lava. The stratigraphic position of the present cephalopod-bearing

reddish shale is considered to correspond to the ammonoid horizon of Audley-Charles (1968, p. 6, fig. 2, columnar section of the Cribas Anticline), about 150 m below the top of the Atahoc Formation. Since Grunau (1953, 1956) first assigned this formation to the Sakmarian (Lower Permian) based on ammonoids, a number of subsequent workers have given support to this determination (e.g., Schouppé, 1957; Shimizu, 1966; Audley-Charles, 1968). More recent and detailed paleontological research by Nishida *et al.* (1997) revealed co-occurrence of ammonoids with the present orthocerids and bactritid, namely *Somoholites beluenis* (Haniel), *Agathiceras* cf. *sundaicum* Haniel, *Metapronorites timorensis* (Haniel) and *Atsabites weberi* Haniel. They concluded that the fossil horizon corresponds stratigraphically to the boundary between the Somohole and Bitauini Formations in West Timor, the age of which horizon is correlative with near the Sterilitamagian (latest Sakmarian)/Aktastinskian (earliest Artinskian) boundary.

Blendinger *et al.* (1992) stated, on the basis of ammonoids, that a conspecific middle Permian fauna flourished from Timor to the western Mediterranean along the northern margin of Gondwana. We shall not comment on the paleobiogeographic implications of the present result, because knowledge concerning Permian nautiloids and bactritoids in this province is still sparse. Besides a record of a Wordian (early Late Permian) fauna from Oman (Niko *et al.*, 1996), the present paper represents the only other documentation of non-ammonoid cephalopods with modern

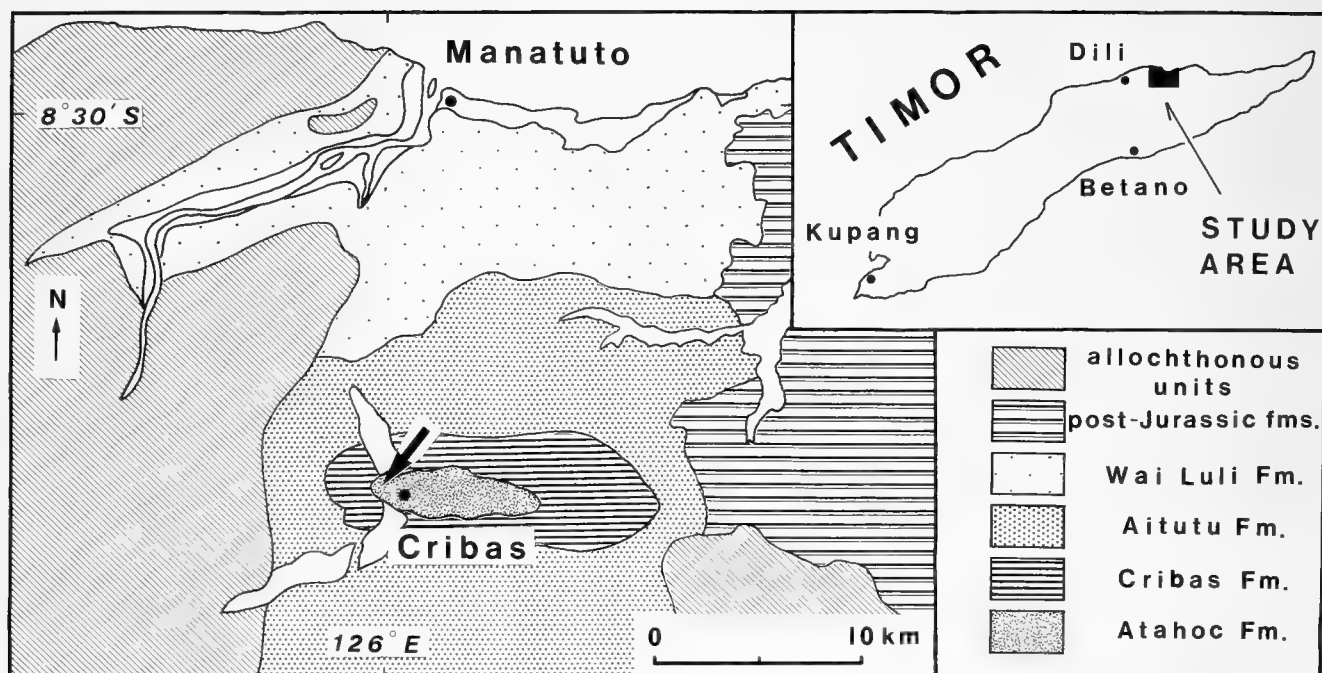


Figure 1. Map showing fossil locality (arrow), and geology of the Cribas area, East Timor (modified from Audley-Charles, 1968).

taxonomic treatment in the northern margin of Gondwana, and therefore provides the base data for paleobiogeography of nautiloids and bactritoids.

The specimens studied are deposited in the paleontological collections of the Department of Geology and Mineralogy, Faculty of Science, Kyoto University (KU).

Systematic paleontology

Subclass Nautiloidea Agassiz, 1847

Order Orthocerida Kuhn, 1940

Superfamily Pseudorthocerataceae Flower and Caster, 1935

Family Pseudorthoceratidae Flower and Caster, 1935

Subfamily Pseudorthoceratinae Flower and Caster, 1935

Genus *Mooreoceras* Miller, Dunbar and Condra, 1933

Type species.—*Mooreoceras normale* Miller, Dunbar and Condra, 1933.

Mooreoceras sp.

Figures 2.1–2.4; 3.9

Description.—Relatively large-sized orthocones with gradual shell expansion, and dorsoventrally depressed, oval cross section; apical end of a fragmentary specimen (KUTMP 20004; Figure 2.2–2.4) is 21.4 mm in dorsoventral diameter and 27.0 mm in lateral diameter, giving a form ratio of 1.26; shell surface lacks annulation, but details are not preserved. Sutures transverse, nearly straight in observable parts; camerae short, maximum dorsoventral

diameter/length ratio approximately 3.4; septal curvature shallow. Siphuncle subcentral, shifted dorsally from center, consists of cyrtochaonic septal necks, 0.70–0.99 mm in length, and inflated connecting rings that are subcylindrical to fusiform in shape; adnation area narrow. Cameral deposits thin, episeptal-mural apically and mural adorally; endosiphuncular deposits weakly developed, form annuli that are unfused and restricted near septal foramina.

Discussion.—Although the surface ornamentation of the examined specimens is not observable, their oval shell cross sections, short camerae, inflated connecting rings with the narrow adnation area and unfused annuli of the endosiphuncular deposits are the characteristics of *Mooreoceras*.

This discovery is of particular interest as one of the relatively rare records of Permian *Mooreoceras*, which also occurs in Early Permian faunas of the Blaine and Dog Creek Formations in Texas (*Mooreoceras "normale"* and *M. gigantea* Clifton, 1942), the Callytharra Limestone in West Australia (*Mooreoceras* sp., Teichert, 1951; Teichert and Glenister, 1952), and the Barfield Formation in East Australia (*Mooreoceras australis* Waterhouse, 1987).

Material.—KUTMP 20003, 40.2 mm in length, and KUTMP 20004, 47.2 mm in length; both are incomplete phragmocones.

Subfamily Spyroceratinae Shimizu and Obata, 1935
Genus *Atahoceras* gen. nov.

Type species.—*Atahoceras timorensis* sp. nov.

Diagnosis.—Like *Bitauioceras* but differs by apparent



Figure 2. *Mooreoceras* sp. 1. KUTMP 20003, longitudinal polished section, showing details of siphuncle, $\times 7$. 2–4. KUTMP 20004; 2. ventral view, $\times 1.5$; 3. Lateral view, venter on left, $\times 1.5$; 4. Septal view of apical end, venter down, $\times 1.5$.

changes in surface ornamentation; i.e., only transverse lirae on juvenile shell, then strongly oblique ridges are added, and reticulated ridges with ribs on the most adoral shell; constriction absent.

Etymology.—The generic name is derived from the Atahoc Formation, in which the type specimens were found.

***Atahoceras timorens* sp. nov.**

Figure 3.1–3.8

Diagnosis.—As for the genus.

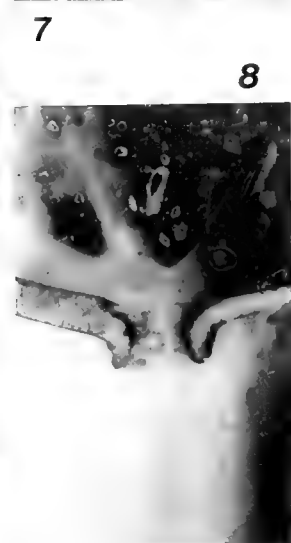
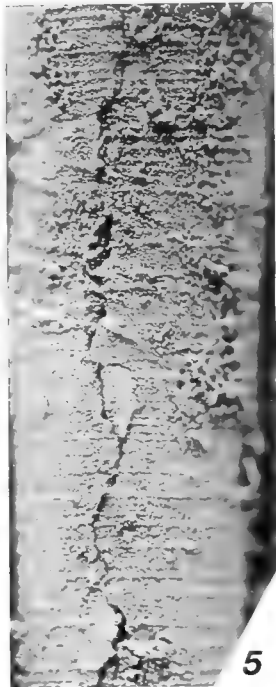
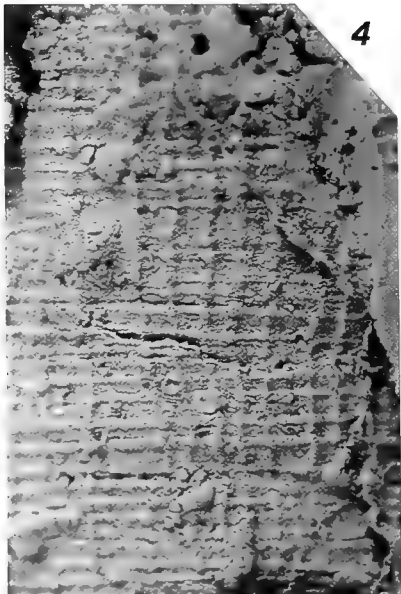
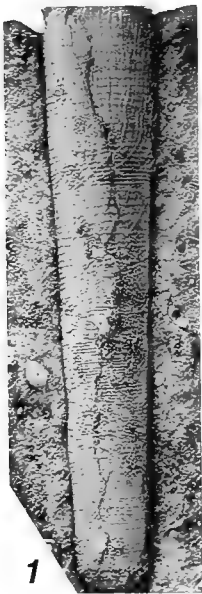
Description.—Orthoconic shells with circular cross section, gradual shell expansion; angle of shell expansion ranges from 4.8° to 5.5° ; largest specimen (holotype; Figure 3.2–3.4, 3.7, 3.8) of phragmocone reaches 17.5 mm in diameter. Surface ornamentation apparently changes with shell growth: 1) only transverse lirae of somewhat unequal size in juvenile shell (up to 3.9 mm in shell diameter), 2) apically strongly oblique and adorally longitudinal ridges that are absent for approximately 5 mm in shell length, but immediately are succeeded by similar ridges, in addition transverse and relatively strong lirae, 3) longitudinal ridges, broad transverse ridges, in addition very weak lirae are also present in interspaces of transverse ridges (beyond 4.5 mm in shell diameter), then 4) longitudinal ridges, and transverse ornamentation consists of ridges and broad, annulation-like but subdued ribs; these ridges form a reticulate pattern (at least up to 11.5 mm in shell diameter); strong sinuation in transverse ornamentation not recognized; transverse constrictions caused by shell thickening and surface constriction are absent. Sutures straight, directly transverse in apical shell; adoral sutures not observed, but weak obliquity of approximately 5° to rectangular direction of shell axis recognized in longitudinal section; strongly concave septa form

long camera, with maximum width/length ratio approximately 1.4 in most adoral camerae; mural part of septum relatively wide. Siphuncle central in position, narrow; septal necks suborthochoanitic, short, 0.9 mm in length in well-preserved septal necks of holotype; connecting ring not preserved; ratio of outside diameter of septal neck/corresponding shell diameter approximately 0.08. Cameral and endosiphuncular deposits not detected.

Discussion.—The surface ornamentation of the juvenile shell, the septal neck structure and the cameral form of *Atahoceras* gen. nov. are in common with *Bitaunioceras* (Shimizu and Obata, 1936), which is based on *Orthoceras bitauniense* Haniel (1915, pl. 56, figs. 5a–c) from the Bitau Formation in West Timor. The diagnostic features of *Atahoceras* appear in the adoral shell, where the changes in surface ornamentation and the absence of the constrictions separate the new genus from *Bitaunioceras*. Except for its possessing periodic surface constrictions and salients, *Bitaunioceras elegantulum* (Gemmellaro, 1890, pl. 11, figs. 12–17; Niko and Nishida, 1987) from the Lower Permian of Sicily is more similar to *Atahoceras timorens* sp. nov. in having the longitudinal ornamentation than the other *Bitaunioceras* species. Ontogenetic changes in the surface ornamentation of this Sicilian species are unknown.

Haniel (1915, pl. 56, figs. 3a–c, 4) described "*Orthoceras welteri*", which has the reticulate ornamentation, from the Bitau Formation. Owing to the lack of detailed information about its internal structure and juvenile shell morphology, the generic assignment of this species is uncertain in modern classification. However, sinuation of its transverse surface ornamentation distinguishes "*O. welteri*" from *A. timorens* sp. nov. at the species level.

Reticulate ornamentation is recognized in some genera belonging to Pseudorthoceratidae, Orthoceratidae and



Geisonoceratidae. Among them, a Carboniferous pseudorthoceratid *Sueroceras* (Riccardi and Sabattini, 1975; type species, *S. irregulare* Riccardi and Sabattini, 1975, pl. 22, figs. 1–12, from Argentina), which has a relatively similar pattern to *Atahoceras*. However, its internal structure, such as partly cyrtocoanitic septal necks, shorter camerae, and thick lining deposits in the siphuncle, suggests that *Sueroceras* has a close phylogenetic relationship with *Dolorthoceras* (Miller, 1931) rather than with *Bitauinoceras* and *Atahoceras*.

Etymology.—The specific name refers to the island of Timor.

Material.—The holotype, KUTMP 20001, is an incomplete phragmocone 68.9 mm in length. In addition, a single paratype 26.2 mm in length, KUTMP 20002, that represents a more apical phragmocone than the holotype.

Subclass Bactritoidea Shimanskiy, 1951
Order Bactritida Shimanskiy, 1951
Family Bactritidae Hyatt, 1884

Genus and species indeterminate

Figure 3.10

Discussion.—This species is represented by a single specimen of a longitudinal thin section. Its diagnostic features are as follows: initial camera (protoconch) subcircular in section, 0.51 mm in diameter, 0.48 mm in length, in conjunction with probably cylindrical second to third developmental stages of phragmocone; adoral diameter of second camera smaller than that of initial camera, 0.37 mm; first three septa recognized, but they and their septal necks are not well preserved.

The general shape and size of the initial camera of the present species are characteristic to the family Bactritidae as shown by Clarke (1894), Erben (1964) and Mapes (1979). Haniel (1915) reported two orthoconic forms, "*Orthoceras*" sp. indet. Nr. 2 (fig. 38) and "*O.*" sp. indet. Nr. 3, which have marginal siphuncular positions, from the Bitauini Formation. Although they may be assignable to the family Bactritidae in modern terms, the materials are too incomplete to discuss relationships with this species.

Material.—KUTMP 20005, 1.0 mm in length, is an apical phragmocone with a complete initial camera.

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← **Figure 3.** 1–8. *Atahoceras timorense* gen. and sp. nov. 1, 5, 6. Paratype, KUTMP 20002; 1. Side view, silicone rubber cast, $\times 3$; 5. Details of apical surface ornamentation, silicone rubber cast, $\times 10$; 6. Details of adoral surface ornamentation, silicone rubber cast, $\times 10$. 2–4, 7, 8. Holotype, KUTMP 20001; 2. Longitudinal thin section, $\times 2$; 3. Transverse polished section at apical end, $\times 2$; 4. Details of surface ornamentation, silicone rubber cast, note reticulated ridges and subdued ribs, $\times 10$; 7. Longitudinal thin section, showing details of siphuncle, $\times 7$; 8. Longitudinal polished section, showing details of septal neck, $\times 10$; 9. *Mooreoceras* sp., KUTMP 20003, longitudinal polished section, $\times 2$; 10. Bactritidae, genus and species indeterminate, KUTMP 20005, longitudinal thin section, $\times 40$.

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A new species of *Ancistrolepis* (Gastropoda: Buccinidae) from the Iwaki Formation (lower Oligocene) of the Joban coal field, northern Japan

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Abstract. *Ancistrolepis* (*Ancistrolepis*) *iwakiensis* sp. nov. from the lower Oligocene of the Joban coal field, northern Japan closely resembles both *Ancistrolepis* (A.) *matchgarensis* (Makiyama) from the upper Eocene to Oligocene of Sakhalin and *Ancistrolepis* (A.) *rategiensis* Titova from the upper Eocene of northwestern Kamchatka. A. (s.s.) *iwakiensis* sp. nov. documents an early evolutionary history of *Ancistrolepis* (s.s.) that appeared in the northwestern Pacific during late Eocene time.

Key words: *Ancistrolepis*, early Oligocene, Gastropoda, northwestern Pacific

Introduction

The Ancistrolepidinae is one of the most common groups of the gastropod family Buccinidae: it occurs in shallow to deep waters in the boreal and arctic regions. Unlike some other buccinids, the fossil and living species of Ancistrolepidinae have a restricted distribution, being found only in the northern Pacific. The systematics of the subfamily is still not clearly understood (Amano *et al.*, 1996).

According to Egorov and Barsukov (1994), who studied the living species of Ancistrolepidinae, the subfamily contains six genera: *Ancistrolepis* (with three subgenera: *Ancistrolepis* (s.s.), *Bathyancistrolepis*, and *Clinopegma*), *Pseudoliomesus*, *Neancistrolepis*, *Sulcosinus*, *Japellion*, and *Parancistrolepis*. The species of *Ancistrolepis* (s.s.) live at present in lower sublittoral to bathyal waters (100 to 690 m) around Honshu, Hokkaido, Sakhalin, and Kamchatka (Higo and Goto, 1993). In addition, *Ancistrolepis* (A.) *vietnamensis* Sirenko and Goryachev has been recorded at depths from 400 to 700 m in the South China Sea (Egorov and Barsukov, 1994).

Titova (1993) discussed the evolution of the fossil Ancistrolepidinae in the northern Pacific, and adopted the systematics of Ancistrolepidinae as follows: *Ancistrolepis* (with *Ancistrolepis* (s.s.), *Bathyancistrolepis*, and *Clinopegma*), *Neancistrolepis*, and *Pseudoliomesus*. She suggested that *Ancistrolepis* (s.s.) appeared in the northwestern Pacific (northern Japan to Kamchatka) during the late Eocene. However, the Paleogene Ancistrolepidinae are rather scarce in the northern Pacific. Matsui (1958) described the earliest representatives of Ancistrolepidinae in Japan from the Urahoro and Ombetsu Groups (upper

Eocene to lower Oligocene) of the Kushiro coal field, eastern Hokkaido, placing the species in *Neptunea*. These species are here referred as *Ancistrolepis* (A.) *huruhatai* (Matsui), A. (A.) *subcarinatus* (Matsui), and A. (*Bathyancistrolepis*) *sitakaraensis* (Matsui). Honda (1989) also originally described *Ancistrolepis* (A.) *ogasawarai* as a *Neptunea* from the Charo Formation (lower Oligocene) of the Ombetsu Group. In addition, *Ancistrolepis* (A.) *modestoideus* (Takeda) has been recorded from the Poronai Formation (upper Eocene to lowermost lower Oligocene) of the Ishikari coal field, central Hokkaido, and the Urahoro and Ombetsu Groups (Takeda, 1953; Matsui, 1958; Honda, 1989).

The southernmost area yielding Paleogene *Ancistrolepis* (s.s.) is located in the Joban coal field, northeastern Honshu, northern Japan (Figure 1). Only two poorly preserved specimens of *Ancistrolepis* (s.s.) have been recorded from the lower Oligocene of the Joban coal field. They are *Ancistrolepis* sp. cf. A. (A.) *subcarinatus* (as *Neptunea ezoana* Takeda; Kamada, 1962, p. 166, pl. 20, fig. 19) from the Iwaki Formation and *Ancistrolepis* (A.) sp. (as A. *yamanei* Kanehara, 1937, p. 13, pl. 4, fig. 8, in part) from the Asagai Formation (Titova, 1993).

Yanagisawa *et al.* (1989) studied the subsurface litho- and biostratigraphy of the Cenozoic strata in the Futaba area of the Joban coal field (Figure 1). Their drill core A-1 yielded numerous well-preserved molluscan fossils at seven horizons of the Iwaki (IW-1-3) and Asagai (AS-1-4) Formations (Figure 2). The mollusks include *Acila* (*Truncacila*) *oyamadensis* Hirayama, *Cyclocardia laxata* (Yokoyama), *Clinocardium asagaiense* (Makiyama), *Papyridea* (*Profulvia*) *harrimani* Dall, *Mya* sp., and *Turritella* sp. (Yanagisawa *et al.*, 1989). In this paper, I describe a new species of

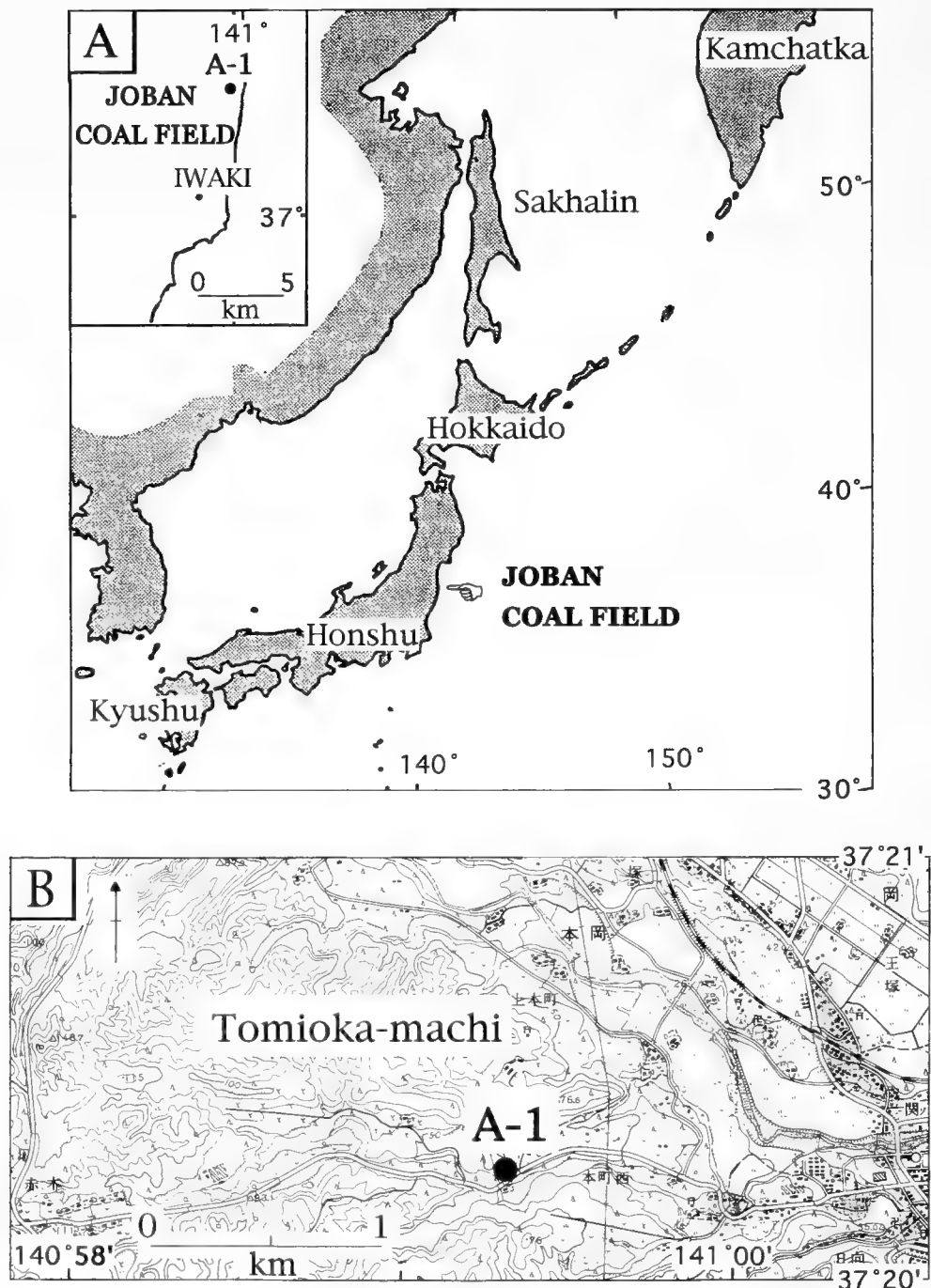


Figure 1. A. Map of the northwestern Pacific showing the location of the Joban coal field and place names referred to in the text. B. Map of the Joban coal field showing the location of drill core A-1 (parts of 1:25,000 scale maps, "Iwaki-Tomioka" and "Yonomori" published by the Geographical Survey of Japan).

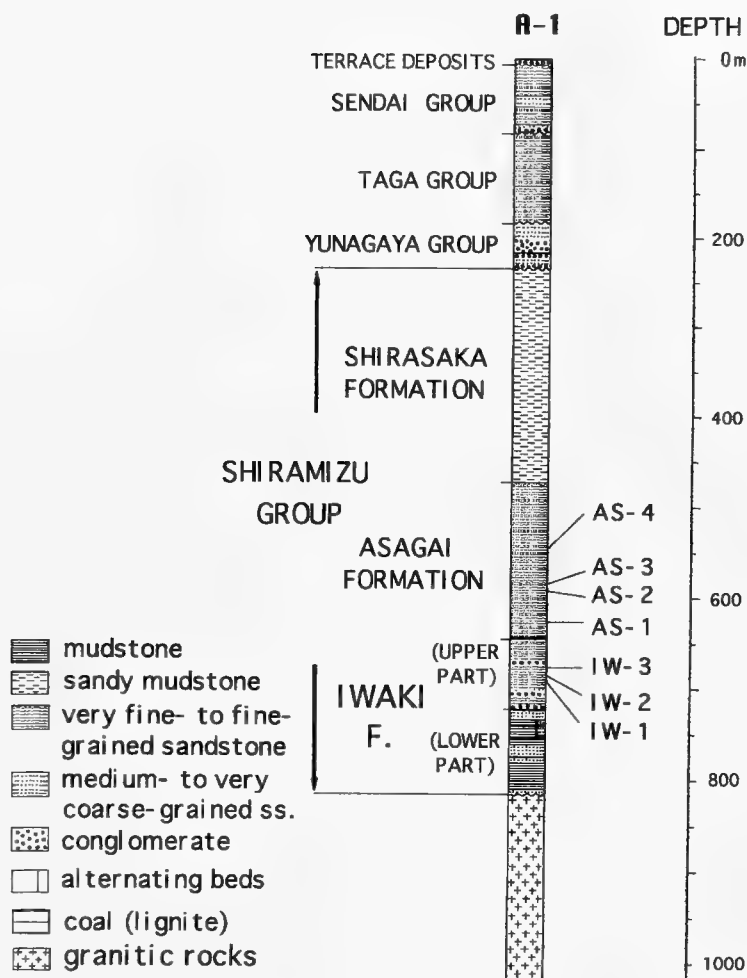


Figure 2. Columnar section of drill core A-1 (compiled from Yanagisawa *et al.*, 1989; Kubo *et al.*, 1994). IW-1-3, AS-1-4; fossil horizons.

Ancistrolepis (s.s.) obtained from the horizon IW-3 of the Iwaki Formation in drill core A-1.

Geological setting

Drill core A-1 of Yanagisawa *et al.* (1989) is lithologically divided into six units, which are, in ascending order, the basement granitic rocks (pre-Tertiary), the Shiramizu (lower Oligocene), Yunagaya (lower Miocene) and Taga (middle to upper Miocene) Groups, the upper part of the Sendai Group (upper Pliocene), and terrace deposits (Pleistocene) (Yanagisawa *et al.*, 1989; Kubo *et al.*, 1994; Figure 2).

The Shiramizu Group is further divided into the Iwaki, Asagai, and Shirasaka Formations, in ascending order (Figure 2). The lower part of the Iwaki Formation consists largely of mudstone with intercalating arkose, fine- to medium-grained sandstone, coal seams, and coaly mudstone. The upper part of the formation is composed of silty, very fine- to fine-grained sandstone with intercalated fine- to medium-grained sandstone and coal seams (Yanagisawa *et al.*,

1989). The Asagai Formation is made up of massive, very fine- to fine-grained sandstone with small carbonaceous fragments. The Shirasaka Formation consists of grey sandy mudstone (Yanagisawa *et al.*, 1989).

Tomida (1986) dated the Iwaki Formation as early Oligocene by the occurrence of the mammalian fossil *Entelodon*. Using fossil diatoms and silicoflagellates, Yanagisawa *et al.* (1989) also dated the Shirasaka Formation as early Oligocene. Consequently, the Shiramizu Group as a whole should be attributed to the lower Oligocene (Yanagisawa *et al.*, 1989).

Description of new species

Family Buccinidae Rafinesque, 1815
Subfamily Ancistrolepidinae Habe and Sato, 1972
Genus *Ancistrolepis* Dall, 1895
Subgenus *Ancistrolepis* s.s.

Type species.—*Chrysodomus eucosmius* Dall, 1891

***Ancistrolepis (Ancistrolepis) iwakiensis* sp. nov.**

Figure 3

Neptunea sp., indet. Yanagisawa *et al.*, 1989, pl. 12, fig. 6.

Type locality.—At a depth of 675.00 to 675.20 m in drill core A-1 (GSJ B326), along a tributary of the Tomioka-gawa, Honcho-nishi, Tomioka-machi, Futaba-gun, Fukushima Prefecture, Japan (Lat. 37°20'16"N, Long. 140°59'20"E; Figure 1B).

Holotype.—GSJF15135 (Figure 3) in the Geological Museum, Geological Survey of Japan, Tsukuba, Japan.

Etyymology.—The name is derived from the formation name "Iwaki."

Material.—One specimen (holotype GSJF15135).

Diagnosis.—Shell moderate in size and fusiform. Spire high, with five whorls. Surface sculptured with three (four on penultimate whorls) subrounded spiral cords. Each interspace occupied by one fine cord.

Description.—Shell moderate in size, rather thin, and fusiform. Whorls five in number, and divided by moderately incised suture. Whorl profile moderately convex with rounded shoulder. Surface sculptured with spiral cords, which intersect feeble growth lines. Three spiral cords on upper whorls, four on fourth (penultimate) whorl, equally spaced, subrounded, and narrower than interspaces. Each interspace on third to fourth whorls occupied by one fine cord. Four spiral cords on upper part of body whorl, subrounded, and narrower than interspaces. More than six spiral cords on lower part, very low, subrounded, and much broader than interspaces. Each interspace on upper part of body whorl occupied by one fine cord.

Measurements.—Holotype, GSJF15135, height 56.5 mm+, diameter 34.7 mm, pleural angle 36°.

Horizon.—IW-3, upper part of the Iwaki Formation (Figure 2). Lower Oligocene.

Associated fauna.—The new species is associated with *Clinocardium asagaiense* (Yanagisawa *et al.*, 1989).

Remarks.—One rather well-preserved, nearly complete specimen, with pale brown shell material, was obtained from the greenish-grey, fine-grained sandstone of the upper part of the Iwaki Formation. The specimen largely lacks the siphonal area, because the core diameter is limited to approximately 60 mm. The features of the siphonal area are therefore not observable.

The new species resembles *Ancistrolepis* (*A.*) *matchgarensis* (Makiyama, 1934) from the Matchigar Formation (upper Eocene to Oligocene; Barinov and Gladenkov, 1998) of northern Sakhalin and the Arakai Formation (Oligocene) of southern Sakhalin (Titova, 1993). *Ancistrolepis matchgarensis* has only three primary cords, however, the new species has both three or four primary cords and one secondary cord. Titova (1993, p. 12, figs. 2A-D) described *Ancistrolepis* (*A.*) *rategiensis* from the Rategian Formation (upper Eocene) of northwestern Kamchatka. The present new species differs from *A. rategiensis* in having more broadly rounded spiral cords. *Ancistrolepis iwakiensis* sp. nov. also differs from *A. (A.)* sp. (= *Ancistrolepis yamanei* Kanehara, 1937, p. 13, pl. 4, fig. 8, in part; see Titova, 1993) from the Asagai Formation in

having a less convex whorl profile and a fine cord between the spiral cords.

Discussion

The genus *Ancistrolepis* (s.s.) is the earliest representative of the Ancistrolepidinae, which probably originated from a common ancestor with the *Neptunea altispirata* group (Titova, 1993). *N. altispirata* was originally described by Nagao (1928) from the Doshi Formation (upper Eocene to lowermost lower Oligocene Funazuan stage; Honda, 1994) of Kyushu, southern Japan. *N. altispirata* has also been recorded from the upper Eocene of western Kamchatka (Gladenkov *et al.*, 1991). The *N. altispirata* group includes *N. onbetsuensis* Matsui from the Omagari and Charo Formations (uppermost upper Eocene to lower Oligocene) of the Kushiro coal field, eastern Hokkaido, and *Neptunea vinjukovi* Krishtofovich from the Oligocene of northern Sakhalin (Titova, 1993). The new species is similar to species of the *N. altispirata* group in having a rather moderately elevated spire.

Honda (1991, 1994) noted that several cold-water genera such as *Neptunea*, *Clinocardium*, and *Mya* appeared from tropical or subtropical ones of Japan and Sakhalin from late middle Eocene to early Oligocene time. Titova (1993) also noted that *Ancistrolepis* (s.s.) appeared in the region of northern Japan to Kamchatka during late Eocene time. These four genera originated in the northwestern Pacific, probably concurrent with the Eocene-Oligocene transition to a global cooling trend.

Titova (1993) divided *Ancistrolepis* (s.s.) into the *Ancistrolepis eucosmius* and *A. grammatus* stocks. The *A. eucosmius* stock is characterized by having a smaller shell, less numerous and weaker radial cords than the *A. grammatus* stock. Accordingly, the new species belongs to the *A. grammatus* stock based on general features of the shell. Titova (1993) further subdivided the *A. eucosmius* stock from the late Eocene to early Miocene into three groups. These are: 1) the *Ancistrolepis huruhatai-A. subcarinatus* group from the upper Eocene and lower Oligocene of Hokkaido and northern Honshu; 2) the *Ancistrolepis rategiensis-A. matchgarensis* group from the upper Eocene and Oligocene of northern Honshu, Hokkaido, Sakhalin, and Kamchatka; and 3) the group of *Ancistrolepis clarki* Tegland and *A. rearensis* (Clark) from the Oligocene and lower Miocene of Northwest America, which probably evolved from *A. rategiensis*. The *A. huruhatai-A. subcarinatus* group is characterized by well-developed secondary spiral cords (Titova, 1993). The new species has only one secondary cord, so it belongs to the *A. rategiensis-A. matchgarensis* group of Titova (1993).

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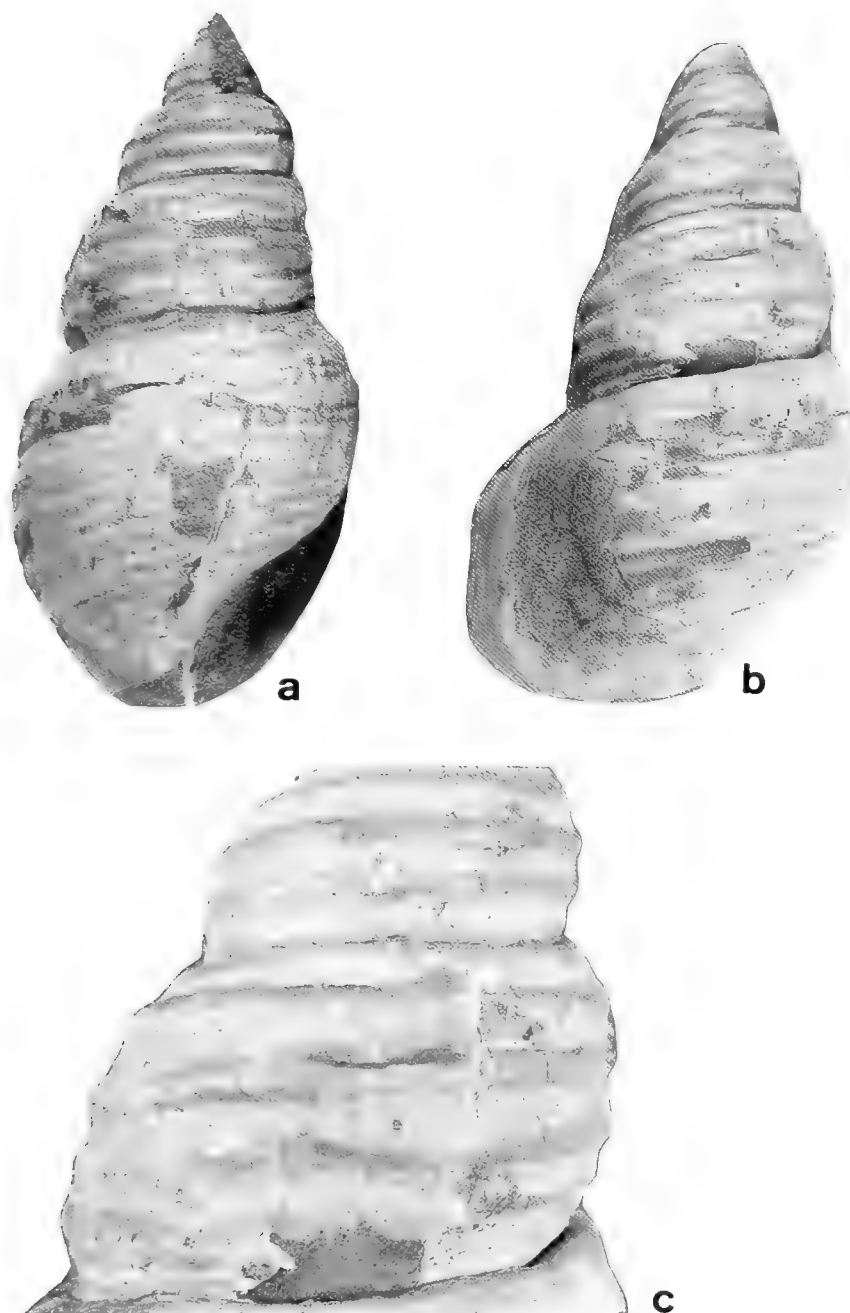


Figure 3. *Ancistrolepis* (*Ancistrolepis*) *iwakiensis* sp. nov., Horizon IW-3, Holotype, GSJF15135. **a.** Apertural-backside view, $\times 1.5$. **b.** Backside view, $\times 1.5$. **c.** Close-up of the third to fourth (penultimate) whorls, $\times 3.1$. GSJ; Geological Museum, Geological Survey of Japan, Tsukuba, Japan.

are expressed to Yukio Yanagisawa (Geological Survey of Japan), for providing the opportunity to study the specimen. Thanks are also expressed to Louie Marincovich, Jr. (California Academy of Sciences), for critical review of the manuscript, and to Paul Callomon (Else Scientific Publications), for proofreading an early draft of the manu-

script.

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Carbon-isotope stratigraphy and its chronostratigraphic significance for the Cretaceous Yezo Group, Kotanbetsu area, Hokkaido, Japan

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Abstract. A positive carbon isotopic excursion across the Cenomanian/Turonian boundary in the Kotanbetsu area, Hokkaido, Japan provides accurate positioning of the boundary. A microscopic study based on organic petrology reveals that the organic matter included in mudstones of the Kotanbetsu River section is exclusively terrestrial. The results of stratigraphic time-series analysis of stable carbon isotopes from these mudstone samples can be translated as representing an average of a terrestrial plant community signal. The isotopic fluctuation through this time interval records information on the global ocean-atmosphere system. Two internationally recognized events characterize the uppermost Cenomanian through middle Turonian. On the basis of this study the Cenomanian/Turonian boundary can be recognized within a stratigraphic range of ~14 meters. This horizon of the boundary is concordant with that from biostratigraphy (ammonoids, inoceramids and planktonic foraminifers). Above the middle Turonian strata, the isotopic pattern supports the biochronology of planktonic foraminifers rather than that of inoceramids.

Key words: biostratigraphy, carbon isotope, Cenomanian/Turonian boundary, Coniacian, correlation, Cretaceous, Kotanbetsu, terrestrial organic matter, Yezo Group

Introduction

International chronostratigraphic correlation of the Cretaceous Yezo Group, especially the Cenomanian through Turonian has been extensively discussed in this decade mainly with reference to the Oyubari area and by the use of megafossils (e.g. Nishida *et al.*, 1993a; Hirano, 1995) and planktonic foraminifers (Motoyama *et al.*, 1991; Hasegawa, 1995, 1997; Takashima *et al.*, 1997). On the other hand, carbon-isotope stratigraphy through the Cretaceous was first shown by Sholle and Arthur (1980) to be a potential correlational tool in the Tethyan region. After this pioneering study, many carbon-isotopic studies using marine carbonate and marine organic matter across the Cenomanian/Turonian (C/T) boundary were performed for detailed correlation at the same resolution as biostratigraphy (e.g. Pratt, 1985; Gale *et al.*, 1993). In Japan, Hasegawa (1995, 1997) analyzed the stable carbon-isotope composition of terrestrial organic carbon from the Oyubari section and discussed its isotope stratigraphy against the control of the planktonic foraminiferal biostratigraphy. Hasegawa

(1995) identified the well-known positive isotopic event caused by an Oceanic Anoxic Event (Schlanger and Jenkyns, 1976) at the C/T boundary and supported the idea that it was a global signal (e.g. Gale *et al.*, 1993; Jenkyns *et al.*, 1994). This was subsequently compared with the carbon-isotope curve derived from marine carbonate carbon established in southern England (Jenkyns *et al.*, 1994) and Italy (Corfield, 1995; Jenkyns *et al.*, 1994). This led to the identification of three isotopic events as global markers for correlation (Hasegawa, 1997). Even though carbon-isotope stratigraphy can be a powerful tool for international correlation (Hasegawa, 1997; Beerling and Jolley, 1998; Gröcke *et al.*, 1999), it has not been employed for detailed stratigraphic positioning of the C/T boundary in other areas of Hokkaido Island except for a study in the Tappu area by Hasegawa and Saito (1993). Nishida *et al.* (1992, 1993b) performed detailed biostratigraphy of megafossils and foraminifers along the Kotanbetsu River in the Kotanbetsu area, Hokkaido focusing on the positioning of the C/T boundary. Hatsugai *et al.* (1999) also discussed detailed planktonic foraminiferal biostratigraphy using internationally

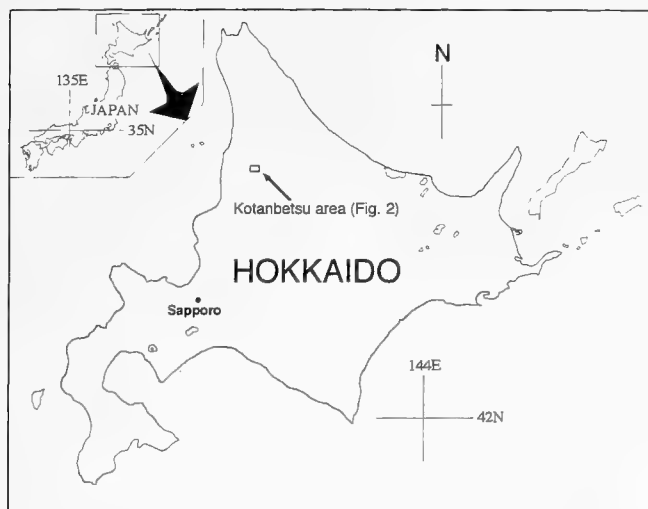


Figure 1. Index map showing the locality of the Kotanbetsu area.

recognized species along the same section.

The purpose of this study is to show how carbon-isotope stratigraphy is a powerful and important tool for correlation. The Kotanbetsu River section was selected as the best section to demonstrate the applicability of carbon-isotope stratigraphy not only for intra-regional but also for inter-regional correlation of the Yezo Group.

Geological setting

The Yezo Group exposed along the Kotanbetsu River in the Kotanbetsu area, Hokkaido, Japan (Figure 1) is interpreted as a forearc basin (Okada, 1979, 1983). The sequence of the Cenomanian through Turonian is represented, in ascending order, by six lithologic units, namely Mf-h, Mi,

Mj-o, Ua-b, Uc-e and Uf-g which were originally defined by Igi *et al.* (1958). These lithologic units strike meridionally and dip westward at an angle of $\sim 60^\circ$. They are nearly continuously exposed and are composed dominantly of dark gray mudstone with either occasional intercalations of sandstone layers of less than 30 cm in thickness or alternating layers of turbiditic sandstone and siltstone. Frequency of intercalating sandstone layers increases in the Units Mi and Ua-b.

The averaged rate of sedimentation for this succession is inferred as approximately 200 m/m.y. based on planktonic foraminiferal biostratigraphy (Hatsugai *et al.*, 1999) using the first occurrence of *Helvetoglobotruncana helvetica* and the first occurrence of the genus *Archaeoglobigerina* and time scale of Gradstein *et al.* (1995). This is more than ten times as fast as the English Chalk section (Jenkyns *et al.*, 1994).

Based on four K-Ar ages from four different bentonite layers encompassing the Unit Mi (Shibata and Miyata, 1978; Shibata *et al.*, 1997), Shibata *et al.* (1997) concluded that the K-Ar age of C/T boundary in the Tappu area was $93.1 \pm 1.2(1\sigma)$. Hirano *et al.* (1997) also obtained similar K-Ar ages from the Tappu and Oyubari sections.

Materials and methodology

Samples were collected along the Kotanbetsu River in the Kotanbetsu area (Figures 1, 2). All samples subjected to isotopic analysis were obtained from the pelagic mudstone unit, whereas turbidite units were ignored. The stratigraphic intervals for samples are between 20–100 m along the section (Figure 2). Powdered mudstones were treated with a 5N solution of HCl for 12 hours to remove carbonate minerals. Each acid-processed sample was then baked in an oven at 850°C for 8 hours in a tube under vacuum together with CuO to convert organic carbon into CO_2 gas. After purification of CO_2 gas on a cryogenic vacuum line, carbon-isotope analyses were performed with a Finnigan MAT

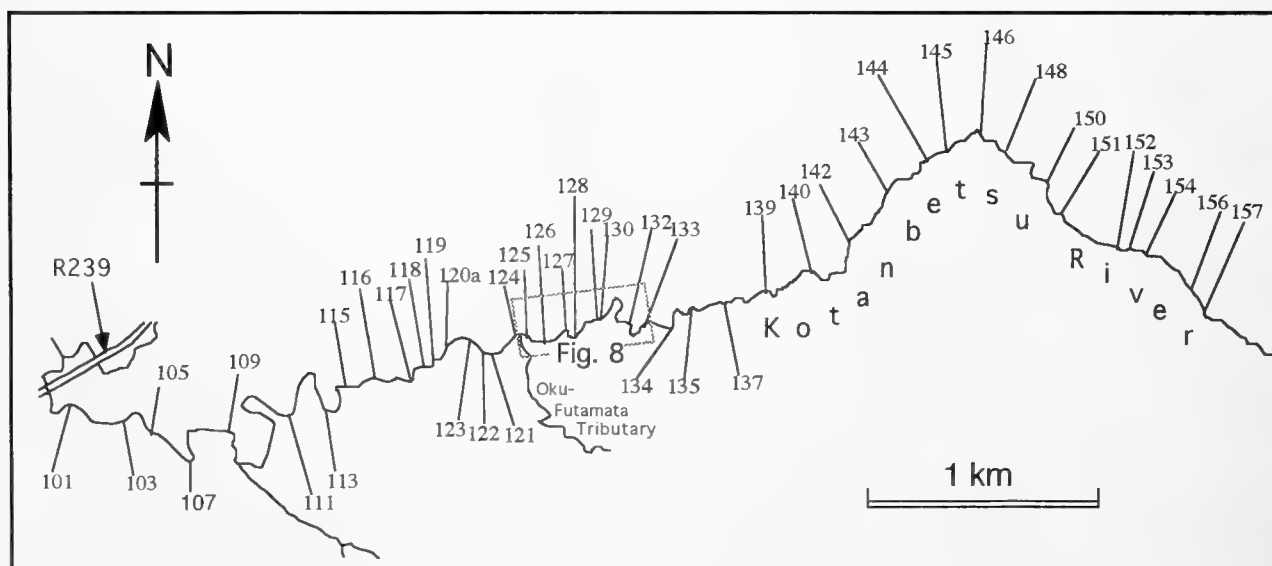


Figure 2. Map showing sampling localities in the Kotanbetsu area.

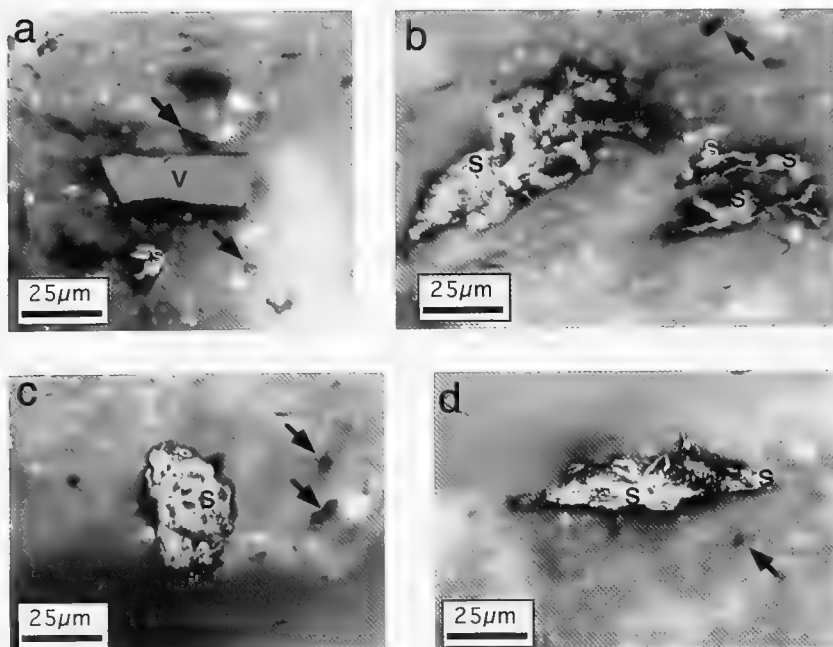


Figure 3. Kerogen observed under microscope with reflected light. Note that most structured particles are identified as semifusinite and vitrinite, which are terrestrial in origin (see text for details). Semifusinites which have obvious lignitic cellular structure in selected samples document vascular plants as their origin. Examples of indeterminate vitrodetrinites and inertodetrinites are also indicated by arrows. **a.** Vitrinite (v) with smaller particles of semifusinite (s) from KOT-148. **b.** Semifusinites (s) with obvious cellular structure from KOT-130. **c.** Semifusinites (s) with obvious cellular structure from KOT-129. **d.** Semifusinites (s) with obvious cellular structure from KOT-101.

delta-E mass spectrometer at Indiana University. The results reported herein are obtained using reference CO_2 as a working standard calibrated by NBS standards. Carbon-isotope results are expressed in the standard delta notation with respect to the PDB standard, where $\delta^{13}\text{C} = \{(^{13}\text{C}/^{12}\text{C})_{\text{sample}} / (^{13}\text{C}/^{12}\text{C})_{\text{standard}} - 1\} \times 1000$, with a reproducibility of analyses of $\pm 0.1\text{‰}$. The isotopic values were checked by an isotopically known laboratory standard (triphenylamine). Total organic carbon (TOC) content of whole rock was estimated by CO_2 gas volume with a Baratron pressure transducer.

For visual observation of kerogen, crushed mudstone was made into polished blocks following the standard preparation procedure (Bustin *et al.*, 1983). Polished pellets were examined using a MPV-2 microscope to identify organic particles.

Results

Visual observation of kerogen

Kerogen was analyzed on selected samples optically under reflected light and in fluorescent mode. Microscopic observation was carried out on seven selected samples (KOT-101, 113, 126, 129, 130, 148 and 152) as representa-

tive horizons of stratigraphically-important isotopic events (see below) through the Kotanbetsu River section. Kerogen from all selected samples is dominated by semifusinite and vitrinite with a minor amount of particulate vitrodetrinite and inertodetrinite (Figure 3a-d) derived exclusively from cellular lignins of terrestrial vascular plants. Preservation of cell structure in semifusinite indicates its origin as woody plant matter. Organic matter of other than terrestrial woody plant origin (alginite and liptinite) was rarely ($\ll 1\%$) detected during microscopic examination. Sporinites, resinites and bitumen were the only fluorescent organic matters in the samples. This fluorescent property can be explained by the absence of marine organic matter. Some nonoxidized vitrinite might have incorporated marine organic molecules through the process of condensation during early stage of diagenesis. But in such a case, marine alginite and/or liptinite should have been more conspicuous components under microscope. The result from visual observation of kerogens strongly suggests no significant incorporation of marine organic materials in the kerogens.

Carbon isotopes and total organic carbon (TOC)

A stratigraphic profile with carbon isotope ratios ($\delta^{13}\text{C}$) for terrestrial organic matter from the Kotanbetsu area is shown

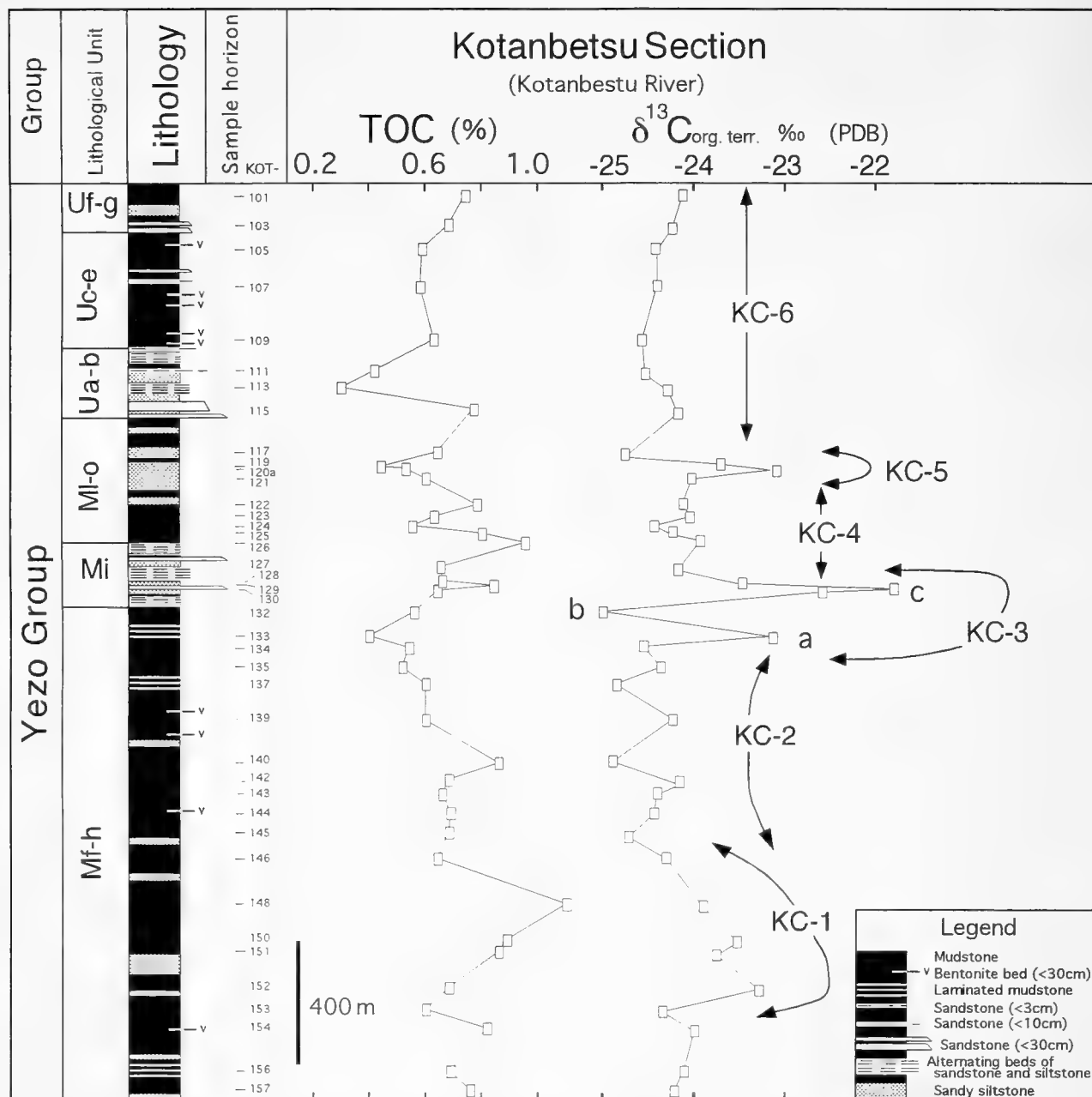


Figure 4. Carbon isotope profile of terrestrial organic matter in the Kotanbetsu River section, Hokkaido, Japan. Labels KC-1 to KC-6 indicate different events on the $\delta^{13}\text{C}$ curve discussed in the text. KC-3 is composed of three subevents namely KC-3a, KC-3b and KC-3c. Note a sharp peak of $\delta^{13}\text{C}$ values (KC-3c) at the middle of the section and a stepwise negative shift through KC-3c~KC-6.

in Figure 4. The profile is divided into six "events" by characteristics in the isotopic fluctuation and are expressed by a KC-numerical notation (designating Kotanbetsu carbon isotopic event):

KC-1: Characterized by a positive isotopic event (-23.3‰) observed in the lower part of Unit Mf-h. Above the peak at KOT-152, $\delta^{13}\text{C}$ shows a gradual negative shift toward -24.7‰ at KOT-145.

KC-2: Segment of relatively negative values fluctuating

between -24.2 and -24.9‰ through the upper Unit Mf-h.

KC-3: Characterized by two positive excursions. At the top of Unit Mf-h, $\delta^{13}\text{C}$ reaches -23.1‰ at the horizon KOT-133 (KC-3a: designated as "a" in Figure 4). However, the value rebounds down to -25.0‰ at KOT-132 just above KOT-133 (KC-3b: designated as "b"). The most prominent feature is a sharp positive excursion of $\sim 2.5\text{--}3 \text{‰}$ which occurs in the middle Unit Mi at the horizon KOT-130 and 129 (KC-3c: designated as "c").

Table 1. Carbon isotopic ratio and TOC along the Kotanbetsu section. The Cenomanian/Turonian boundary is expected just above KOT-129 (see text for details).

| Sample | $\delta^{13}\text{C}$ org. terr. ‰ (PDB) | TOC (%) |
|----------|---|---------|
| KOT-101 | -24.1 | 0.74 |
| KOT-103 | -24.2 | 0.68 |
| KOT-105 | -24.4 | 0.59 |
| KOT-107 | -24.4 | 0.58 |
| KOT-109 | -24.6 | 0.63 |
| KOT-111 | -24.5 | 0.42 |
| KOT-113 | -24.3 | 0.30 |
| KOT-115 | -24.2 | 0.77 |
| KOT-117 | -24.8 | 0.64 |
| KOT-119 | -23.7 | 0.44 |
| KOT-120a | -23.1 | 0.53 |
| KOT-121 | -24.0 | 0.60 |
| KOT-122 | -24.1 | 0.78 |
| KOT-123 | -24.1 | 0.63 |
| KOT-124 | -24.4 | 0.55 |
| KOT-125 | -24.2 | 0.80 |
| KOT-126 | -23.9 | 0.95 |
| KOT-127 | -24.2 | 0.65 |
| KOT-128 | -23.5 | 0.66 |
| KOT-129 | -21.8 | 0.84 |
| KOT-130 | -22.6 | 0.64 |
| KOT-132 | -25.0 | 0.56 |
| KOT-133 | -23.1 | 0.40 |
| KOT-134 | -24.6 | 0.54 |
| KOT-135 | -24.4 | 0.52 |
| KOT-137 | -24.9 | 0.60 |
| KOT-139 | -24.2 | 0.60 |
| KOT-140 | -24.9 | 0.86 |
| KOT-142 | -24.2 | 0.68 |
| KOT-143 | -24.4 | 0.66 |
| KOT-144 | -24.4 | 0.69 |
| KOT-145 | -24.7 | 0.68 |
| KOT-146 | -24.3 | 0.64 |
| KOT-148 | -23.9 | 1.10 |
| KOT-150 | -23.5 | 0.89 |
| KOT-151 | -23.7 | 0.86 |
| KOT-152 | -23.3 | 0.68 |
| KOT-153 | -24.4 | 0.60 |
| KOT-154 | -24.0 | 0.82 |
| KOT-156 | -24.1 | 0.69 |
| KOT-157 | -24.2 | 0.76 |

KC-4: Relatively stable isotopic ratios above KC-3c excursion. $\delta^{13}\text{C}$ drops rapidly above KOT-129 and stabilizes around -24.0‰ between the middle Unit Mi and the middle Unit MI-o.

KC-5: Characterized by a minor positive excursion of

~1‰ at KOT-120 followed by a negative shift back to KC-6.

KC-6: Characterized by stable isotopic ratio between -24.8 and -24.1‰. The most negative value is recorded in the lowest part of this interval (-24.8‰).

Values of total organic carbon content (TOC) range between 0.2 and 1.0% with no notable fluctuation in the Kotanbetsu River section.

Discussion

No organic-rich layer across the C/T boundary

In spite of fine parallel laminations in the Mi Unit indicating limited benthic activity and dysaerobia, no TOC spike (extraordinary accumulation of organic matter) at the C/T boundary (=peak horizon of $\delta^{13}\text{C}$; see following discussion) was observed (Figure 4) contrary to the case of many carbonate sections around the world (e.g. Schlanger *et al.*, 1987). This is caused by the depositional environment of the Kotanbetsu section, which was far different from that of those sections with an accumulation of organic matter at the boundary. The sedimentation rate of the Kotanbetsu section is about 200 m/m.y. and substantially all materials including organic matter are terrestrial in origin. Most of the organic matter in the mudstone samples are very residual lignitic material. Therefore, the concentration of organic matter across the section was controlled predominantly by the content of organic matter in terrigenous debris and never affected by oceanographic events.

Factors controlling carbon-isotope fluctuations

Kerogen from two samples representing the KC-3 event were optically examined and the results were compared with those from KC-4, KC-6 and KC-1. All visually checked samples are dominated by semifusinite and vitrinite. This means organic matter in the samples is derived from nothing but lignins of terrestrial woody C_3 plants which are exclusively resistant to oxidation. Rare occurrences of small amounts of alginite, sporinite, resinite, and bitumen should not affect the following discussion dealing with differences larger than 0.1‰ of carbon isotopic fluctuation. Since these samples were selected from the intervals of major isotopic events of stratigraphic importance, the isotopic fluctuation of terrestrial organic carbon obtained in this study cannot be ascribed to the composition of kerogens. That the lithological evidence shows no significant change of depositional environment also suggests that the composition of kerogens is a feature of the sedimentary rock through the Kotanbetsu River section.

In Figure 5, $\delta^{13}\text{C}$ values are plotted against TOC with no systematic relation revealed between them. This indicates that the $\delta^{13}\text{C}$ values are independent of mechanisms of supply and deposition of organic matter; organic matter derived from lignins of terrestrial woody C_3 plants has not been carbon-isotopically biased by these mechanisms and has essentially kept its original isotopic signature. As mentioned above, the isotopic fluctuation of organic carbon in the Kotanbetsu River section can be interpreted as representing the average biomass of woody plants in the provenance area. The isotopic fluctuation of global atmospheric CO_2 is

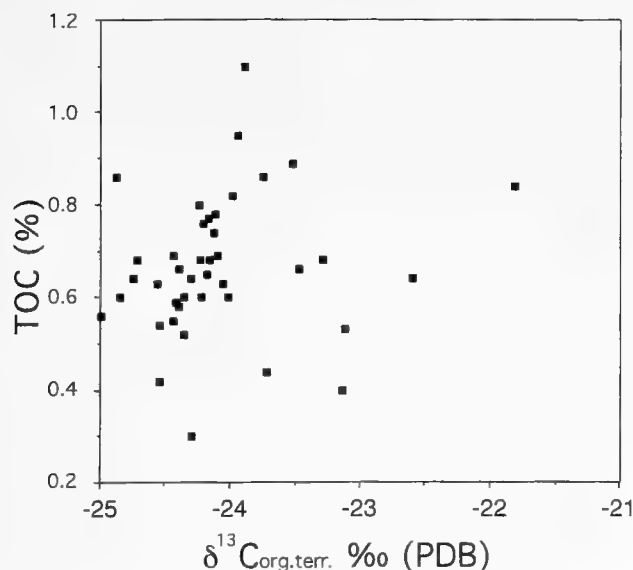


Figure 5. Carbon-isotope ratios of terrestrial organic carbon ($\delta^{13}\text{C}_{\text{org.terr.}}$) against total organic carbon content (TOC; dry weight %) along the Kotanbetsu River section.

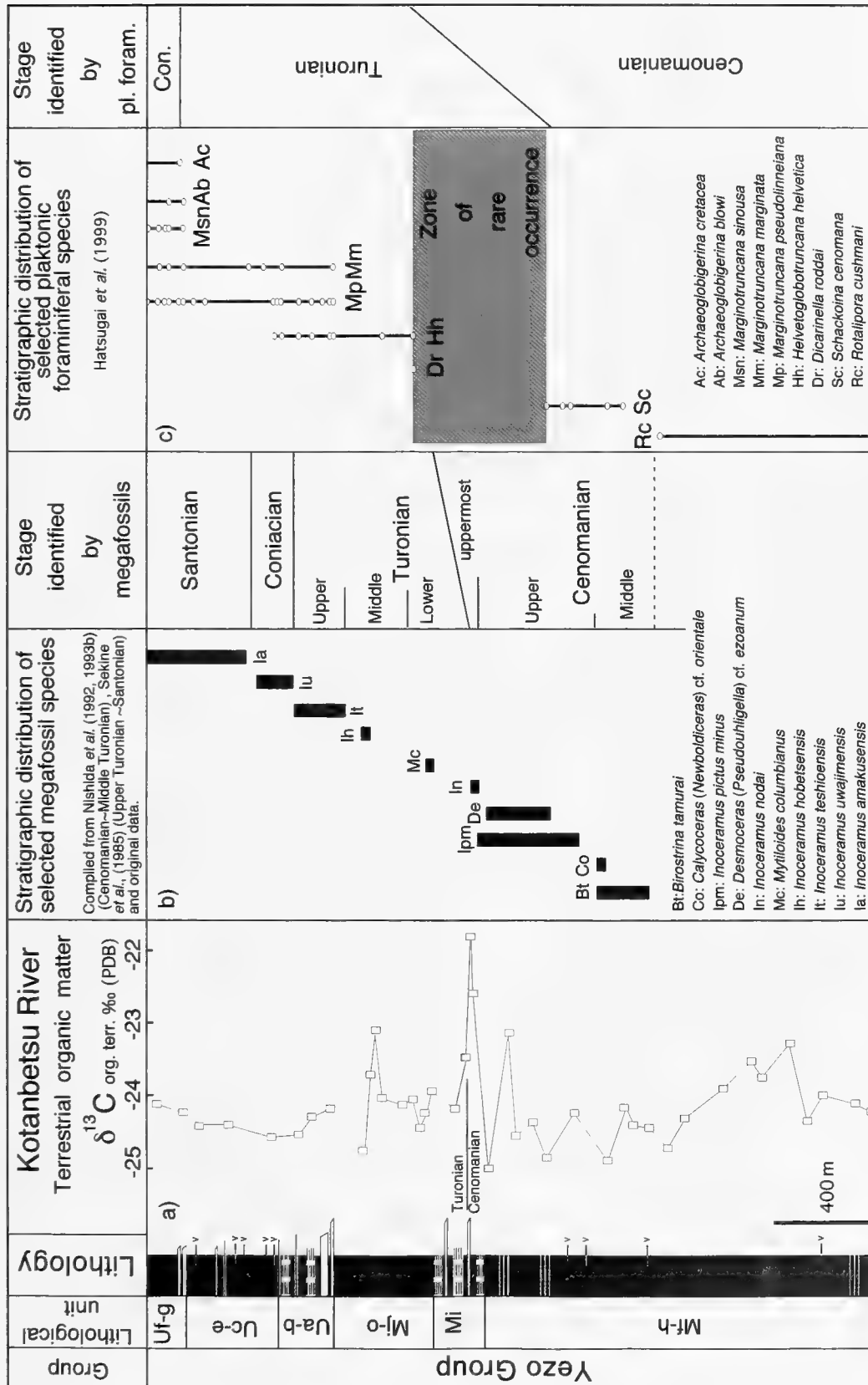
interpreted to be a primary factor responsible for $\delta^{13}\text{C}$ fluctuation of the terrestrial biomass as discussed in Hasegawa (1997), Beerling and Jolley (1998) and Gröcke *et al.* (1999). If this assumption is accepted and other environmental and/or ecological factors are negligible, $\delta^{13}\text{C}$ fluctuation of terrestrial organic matter is essentially parallel to that of carbonates. Arthur *et al.* (1988) ascribed a discrepancy of amplitude observed between marine carbonate and marine organic carbon across the C/T boundary to a marked decrease of partial pressure of CO_2 in the ocean-atmosphere system. Gröcke *et al.* (1999) discussed the possibility that the partial pressure of atmospheric CO_2 may have also affected carbon-isotopic fluctuation of fossil woods as a secondary factor in conjunction with the isotopic composition of CO_2 . If $\delta^{13}\text{C}$ of atmospheric CO_2 during the deposition of the studied sequence exclusively reflects proportion of fluxes of organic and inorganic carbons into/out of the ocean-atmospheric reservoir, changes of partial pressure of atmospheric CO_2 should lead to exaggeration of the $\delta^{13}\text{C}$ events in terrestrial and marine organic matter against marine carbonates (see also discussion of Popp, *et al.*, 1989; Gröcke *et al.*, 1999). Therefore, even if the $\delta^{13}\text{C}$ curve obtained in this study was affected by the partial pressure of atmospheric CO_2 , it is still plausible to correlate it with $\delta^{13}\text{C}$ curves derived from marine carbonates as well as those from terrestrial organic matter of other Hokkaido sections. Kuypers *et al.* (1999) discussed a turnover from a C_3 plant community to a C_4 -dominated community, which had been derived from a decrease of partial pressure of CO_2 , as a factor in an exaggerated $\delta^{13}\text{C}$ excursion of n-alkanes. This factor could only exaggerate a positive excursion of $\delta^{13}\text{C}$. The kerogens examined under the microscope show predominance of lignitic macerals in both samples from the C/T boundary excursion (KOT-129 and 130) and other horizons.

This indicates no turnover of C_3/C_4 plant communities was involved with the $\delta^{13}\text{C}$ excursion at the C/T boundary shown in the present study. Shift of atmospheric humidity and taxonomic turnover in the provenance of organic matter may have affected carbon isotopic fractionation during photosynthesis of the biomass (O'Leary, 1993). These factors could result in some local, regional or sometimes global isotopic disturbance and should be considered during carbon-isotope correlation. Nguyen Tu *et al.* (1999) proposed that environmental stress derived from salinity had affected significantly the carbon isotopic composition of fossil terrestrial plants from Cenomanian strata. However, the organic matter treated in this study is interpreted to have been transported from wide and distant provenance. It should be highly mixed enough to eliminate such a local salt stress discussed in Nguyen Tu *et al.* (1999).

Significance of carbon isotope stratigraphy as a tool for correlation

The Kotanbetsu River section has been subdivided into stages by biostratigraphic studies of megafossils (Nishida *et al.*, 1992, 1993b) and planktonic foraminifera (Nishida *et al.*, 1992; Hatsugai *et al.*, 1999) (Figure 6). No biochronological study of megafossils is available above the middle Turonian along the Kotanbetsu River section. However, Sekine *et al.* (1985) studied the Tappu area next to the Kotanbetsu area and that study was adopted to draw boundaries above the middle Turonian. Planktonic foraminiferal biostratigraphy (Hatsugai *et al.*, 1999) indicates no appreciable diachroneity in lithologies between the Tappu and Kotanbetsu areas.

As Hatsugai *et al.* (1999) noted, stages defined by both megafossils and planktonic foraminifers correspond well with each other below the upper part of Unit Mj-o (Figure 6). There are two conspicuous isotope events (KC-3 and KC-4) in the Kotanbetsu River section which can be correlated internationally (Figure 7). KC-1 is regionally correlated to H1 of the Oyubari section (Figure 7) by its shape and amplitude of isotopic fluctuations as well as by biostratigraphic position (within planktonic foraminiferal *Rotalipora cushmani* Zone). Though this event could be globally correlated, however, it is not conclusive because of low chronological resolution across this event in Japan. KC-2 is the common event of three Hokkaido sections (Oyubari, Tappu and Kotanbetsu; Figure 7) and equivalent to H2 in the Oyubari area (Hasegawa, 1997). This negative isotopic feature of KC-2/H2 cannot be observed in European sequences (Jenkyns *et al.*, 1994). Shift of atmospheric humidity and/or taxonomic turnover in the provenance of organic matter may explain this event, which is specific to terrestrial organic carbon (see O'Leary, 1993). KC-3 is the most prominent feature of the Kotanbetsu River section and is regarded to be the best worldwide stratigraphic marker across the C/T boundary in relation to the Oceanic Anoxic Event II (Schlanger and Jenkyns, 1976; Arthur *et al.*, 1988). KC-3 is composed of a double peak and a trough between (Figure 4). These subevents in KC-3, namely KC-3a, b and c ("a", "b" and "c" in Figure 4) can be correlated with isotopic subevents a, b and c, respectively at the C/T boundary of the Oyubari (Hasegawa, 1995) and Tappu areas (Hasegawa, 1994), al-



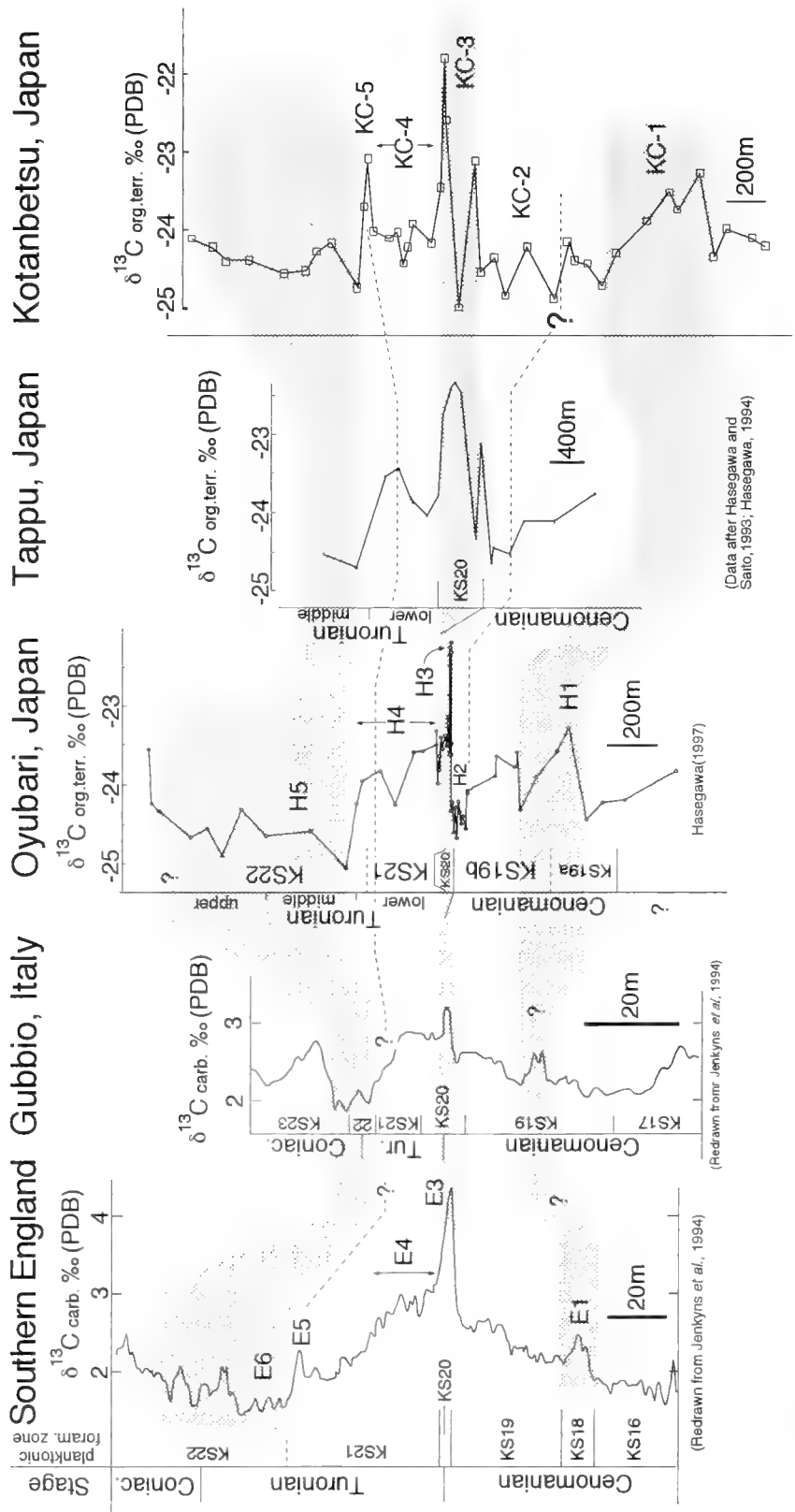


Figure 7. Comparison of carbon-isotope profiles for carbonate (southern England and Gubbio, Italy) and terrestrial organic matter (Oyubari, Tappu and Kotanbetsu sections, Japan). Event notations for southern England and Oyubari are given by Hasegawa (1997). Note the good correlation between the three carbon-isotope events (spike at the C/T boundary, shoulder at the lower Turonian and a minimum at middle or upper Turonian). Biochronology for planktonic foraminifera is based on Caron (1985), Robaszynski and Caron (1979) and Sliter (1989) and for megafossils is based on Toshimitsu *et al.* (1995). $\delta^{13}\text{C}_{\text{carb}}$: carbon-isotope ratio of carbonate; $\delta^{13}\text{C}_{\text{org.terr}}$: carbon-isotope ratio of terrestrial organic matter.

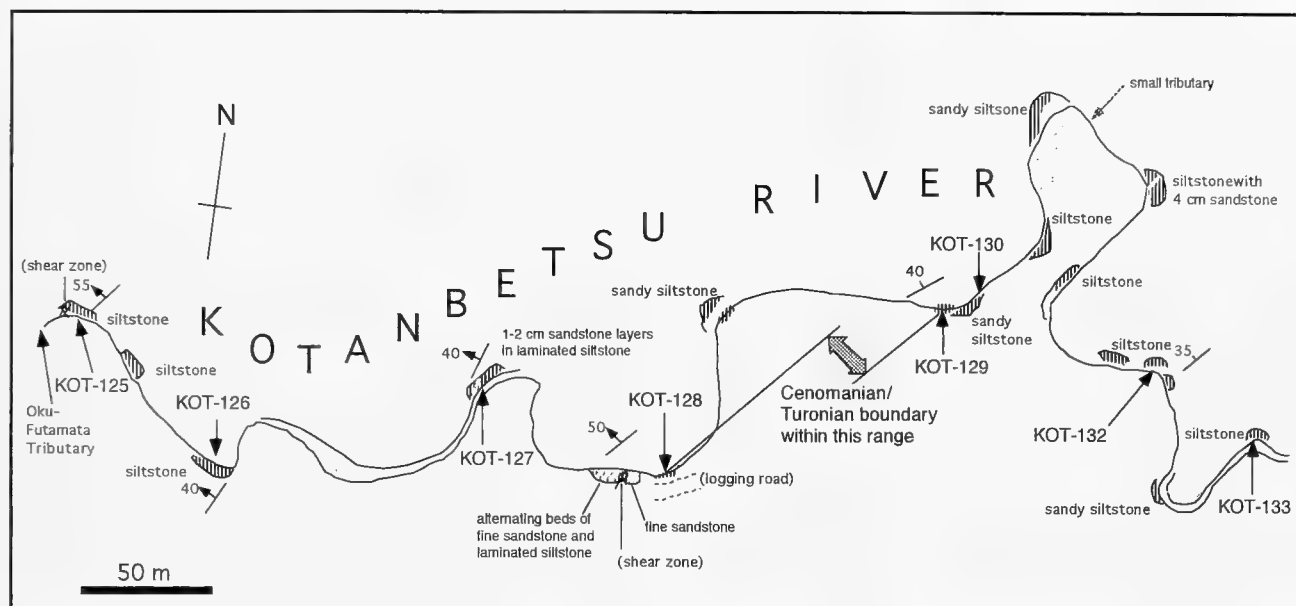


Figure 8. Plan map along the Kotanbetsu River showing detailed position of the Cenomanian/Turonian boundary expected from carbon isotope stratigraphy. The possible boundary is limited stratigraphically within ~ 14 m between KOT-129 and KOT-128.

though inconclusively, due to sparse sampling encompassing KC-3 and difference of amplitude of the subevent KC-3b. Hence it is still open to question whether the entire KC-3 or only KC-3c corresponds to the globally observed carbon isotope excursion at the C/T boundary (see Schlanger *et al.*, 1987). As discussed in detail by Hasegawa (1995), the C/T boundary can be drawn just above the positive $\delta^{13}\text{C}$ excursion; the C/T boundary in the Kotanbetsu River section is drawn just above the horizon of KOT-129 (Figures 6, 8). The horizon of the C/T boundary is stratigraphically limited to ~ 14 m between KOT-129 and KOT-128.

Nishida *et al.* (1993b) reported occurrences of *Inoceramus nodai* just below KOT-129. In the Oyubari area, *I. nodai* was reported from 10 m below the carbon-isotopic excursion identifying the C/T boundary (Hasegawa, 1995; Nishida *et al.*, 1993a; Hirano, 1995) suggesting *I. nodai* is an important boundary marker in Hokkaido. According to Hatsugai *et al.* (1999), KC-3 is stratigraphically included in a "zone of rare occurrence" of planktonic foraminifera. A similar planktonic foraminiferal event encompassing the carbon isotopic excursion at the C/T boundary is also reported from the Oyubari area (Hasegawa, 1999) and the Tappu area (Hasegawa, 1994) suggesting an environmental deterioration across the boundary. Controlling factors other than $\delta^{13}\text{C}$ fluctuation in the global CO_2 reservoir may have disturbed the stratigraphic position of KC-3 and might have spoilt the discussion above the C/T boundary. In such a case, additional "noise" should be superimposed on the global signal derived from isotopic change of the CO_2 reservoir. Even though such a possibility cannot completely be rejected, KC-3 event showing similar magnitude of $\delta^{13}\text{C}$ excursion to that of carbonate (e. g. Jenkyns *et al.*, 1994; Pratt *et al.*, 1985) and terrestrial organic matter (Hasegawa and

Saito, 1993; Hasegawa, 1997) should contain the least "noise" for correlation of the C/T boundary. Uličný *et al.* (1997) interpreted isotopic fluctuation of organic carbon encompassing parasequence boundary near the C/T boundary based on a steady isotopic ratio of terrestrial organic carbon through the sequence in Bohemia. The present study and Hasegawa (1997) clearly shows that this interpretation cannot be accepted because the major positive "spike" of terrestrial organic carbon exists across the C/T boundary. Based on 200 m/m.y. for sedimentation rate; duration of KC-3 (from KOT-133 to KOT-129) is estimated as 0.73 m.y.

Another international event is KC-4 just above the C/T boundary and is represented by a stable "plateau" of the isotopic curve (Figure 7). Both megafossil and planktonic foraminiferal chronology indicate KC-4 falls in the lower-middle Turonian (Figure 6). Both in the Oyubari and Tappu areas, a similar isotopic event is also recognized. On the isotopic curve of the Kotanbetsu River section, there is a minor positive event (KC-5) above KC-4. A similar feature also exists on the curve from the Tappu section but is diminished in magnitude on the curves from Oyubari (Figure 7). KC-5 could be correlated to E5 of southern England (Figure 7); however, this is not definite because of the insufficient age control and different magnitude of the positive excursion between these areas. Therefore, KC-5 can be either a global signal or a local/regional isotopic perturbation superimposed on the global KC-4 event caused by influx of less mixed (isotopically not averaged) plant debris derived from a narrower provenance.

Contrary to the chronostratigraphic concordance of megafossil and planktonic foraminifera below the middle Turonian, there are considerable discrepancies above it (Hatsugai *et al.*, 1999). Motoyama *et al.* (1991) also discussed a chronostratigraphic discrepancy on the

Turonian/Coniacian boundaries at the Oyubari area between megafossils and microfossils. Even though internationally it is recognized that the total range of *Helvetoglobotruncana helvetica* is limited to the middle Turonian (Robaszynski and Caron, 1979; Caron, 1985; Sliter, 1989), the stratigraphic distribution of *Inoceramus teshioensis* spans the Upper Turonian and *Inoceramus uwajimensis* the Coniacian (Toshimitsu *et al.*, 1995) which all overlap the range of *H. helvetica*. The first occurrence of *Inoceramus amakusensis* is positioned far below the first occurrence of *Margino-truncana sinuosa* (indicating the top of the Turonian; Caron, 1985) and genus *Archaeoglobigerina* (indicating the basal Coniacian; Caron, 1985). They show clear discrepancies with the stratigraphic relationship compiled by Toshimitsu *et al.* (1995) (Figure 6; see also Table 1 of Toshimitsu *et al.*, 1995). As a result, the stages identified by megafossils tend to give a younger age than that identified by planktonic foraminifers. These chronological inconsistencies occur above the top of the stratigraphic range of *I. hobetsensis*. This fact means that stratigraphic distributions of either/both inoceramids (*I. teshioensis*, *I. uwajimensis* and *I. amakusensis*) and/or planktonic foraminifers (*H. helvetica*, *M. sinuosa* and genus *Archaeoglobigerina*) show diachroneity.

Above isotopic profile KC-5, the carbon-isotope ratio reaches a minimum at KOT-117. This horizon can be correlated to the oldest part of the negative isotope event (H5 of the Oyubari section and E6 of the South England section: see Fig. 6 and 8 of Hasegawa, 1997). The steady isotopic ratios between -24.6 and -24.1‰ above horizon KOT-115 suggest that this section does not extend to the upper part of the Santonian. Hasegawa *et al.* (1997) reported a positive carbon-isotope event in the middle Santonian from an equivalent of the Yezo Group in Sakhalin. This Santonian event can be correlated to southern England (Jenkyns *et al.*, 1994) and Italy (Corfield, 1995; Jenkyns *et al.*, 1994). If the Kotanbetsu River section in this study reached the Santonian, the positive excursion should be observed near the top of the stratigraphic column in Figure 6. Comparing general carbon isotopic patterns from southern England and Italy (Corfield, 1995; Jenkyns *et al.*, 1994; Figure 7), the uppermost part of the Kotanbetsu River section studied herein can be interpreted to be the lower part of the Coniacian. This chronological assumption is close to the age assignment by planktonic foraminifera rather than that based on inoceramids.

Conclusion

In order to demonstrate the applicability of carbon-isotope stratigraphy of the Yezo Group for correlation, a stratigraphic time-series isotopic analysis of terrestrial organic carbon was studied from the Cenomanian to Coniacian along the Kotanbetsu River in Hokkaido, Japan. The carbon-isotope curve generated was compared with similar profiles of terrestrial organic carbon from Oyubari and Tappu in Hokkaido (Hasegawa, 1995, 1997) and marine carbonate from southern England and Italy (Jenkyns *et al.*, 1994). The salient conclusions are as follows:

1. The origin of organic carbon is interpreted to be exclusively terrestrial woody plants. Petrographic study on or-

ganic matter in mudstone samples reveals practically no marine organic matter in the seven examined samples. The carbon-isotope ratios of organic matter from the Kotanbetsu River section can be interpreted as that of an average lignitic material from woody plants. Global carbon-isotope events can be recognized in the isotopic curve from Kotanbetsu.

2. Event KC-3 records the isotopic event of the Cenomanian/Turonian boundary. It is still unclear which carbon-isotope event, namely all of KC-3 or only KC-3c, represents the C/T boundary. Notwithstanding this, the Cenomanian/Turonian boundary is drawn just above sample KOT-129, which has the most positive $\delta^{13}\text{C}$ ratio.

3. Event KC-4 is correlated to the event H4/E4 of both the Oyubari and southern England sections.

4. A negative event above KC-5 is correlated to the earliest part of event H5/E6 of Oyubari and southern England.

5. The most plausible chronologic interpretation for the younger part of KC-6 is middle Turonian to Coniacian and supports planktonic foraminiferal evidence rather than that derived from inoceramids. In spite of occurrences of *Inoceramus amakusensis*, the studied succession does not reach the Santonian because the general isotopic pattern differs from that of the Santonian from southern England (Jenkyns *et al.*, 1994) and Sakhalin (Hasegawa *et al.*, 1997).

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Taxonomic revision of *Pisulina* (Gastropoda: Neritopsina) from submarine caves in the tropical Indo-Pacific

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Abstract. Species of the tropical Indo-Pacific gastropod *Pisulina* (superorder Neritopsina), previously known only from empty shells and regarded as a genus of Smaragdiinae (Neritidae), are revised on conchological criteria. *Pisulina* dwells in gloomy to totally dark, tropical and subtropical, shallow-water submarine caves, where their empty shells are ubiquitous. Study of the previously described modern and fossil species and examination of newly collected material from more than 50 submarine caves on Pacific islands show that there are six species in the genus: *P. adamsiana* Nevill and Nevill, 1869 (Holocene), *P. subpacificica* Ladd, 1966 (late Miocene), *P. biplicata* Thiele, 1925 (Recent), *P. maxima* new species (Recent), *P. tenuis* new species (Recent), and *Pisulina* sp. (Pleistocene). An analysis of previously unstudied shell characters (shell form, shell microstructure, protoconch morphology, and opercular features) of *Pisulina* and other modern, representative genera of Neritopsina places the genus close to the freshwater and brackish-water genus *Neritilia*, based on three unique characters (inclined protoconch, spiral ridges on the protoconch surface, and perpendicularly arranged prisms in the outer shell layer), and both genera are herein included in the family Neritiliidae. This study shows that the protoconch and shell microstructure analysis is important for re-evaluating fossil species previously placed in Neritidae.

Key words: Neritiliidae, *Pisulina*, protoconch, shell microstructure, submarine cave

Introduction

Pisulina Nevill and Nevill, 1869 has been a gastropod genus of systematically uncertain placement. Aside from the type species, *Pisulina adamsiana* Nevill and Nevill, 1869, the genus has included one modern species, *Pisulina biplicata* Thiele, 1925, and one fossil species, *Pisulina subpacificica* Ladd, 1966. The species previously have been known only from empty shells, so knowledge of their anatomy, operculum, radula and habitat have been entirely lacking. Empty shells occasionally have been found in beach drift from the tropical western Pacific (Habe, 1963; Hinoide and Habe, 1991; Fukuda, 1993; Loch, 1994; Sasaki, 1998) and have been dredged from 70 m off southern Africa (Herbert and Kilburn, 1991).

Nevill and Nevill (1869) thought the genus was close to

Teinostoma (currently classified in Vitrinellidae of Caenogastropoda; e.g., Ponder and de Keyser, 1998) and *Calceolina* [junior synonym of *Teinostoma* (*Calceolata*); Thiele, 1929] based on overall similarity in shell morphologies. Thiele (1925) was the first author to place *Pisulina* in Neritidae, and this familial allocation was followed in his monograph (Thiele, 1929). Wenz (1938) included *Pisulina* in the subfamily Smaragdiinae Baker, 1923, of Neritidae, and was subsequently followed by Knight *et al.* (1960) and Komatsu (1986). However, Herbert and Kilburn (1991) found that *Pisulina* differs in protoconch morphology not only from *Teinostoma* but also from *Smaragdia*, the type genus of Smaragdiinae. They observed that the change of coiling axis occurs between the larval shell and teleoconch whorls in *P. adamsiana*, although they followed Robertson's (1971) view that this change occurs between the embryonic and

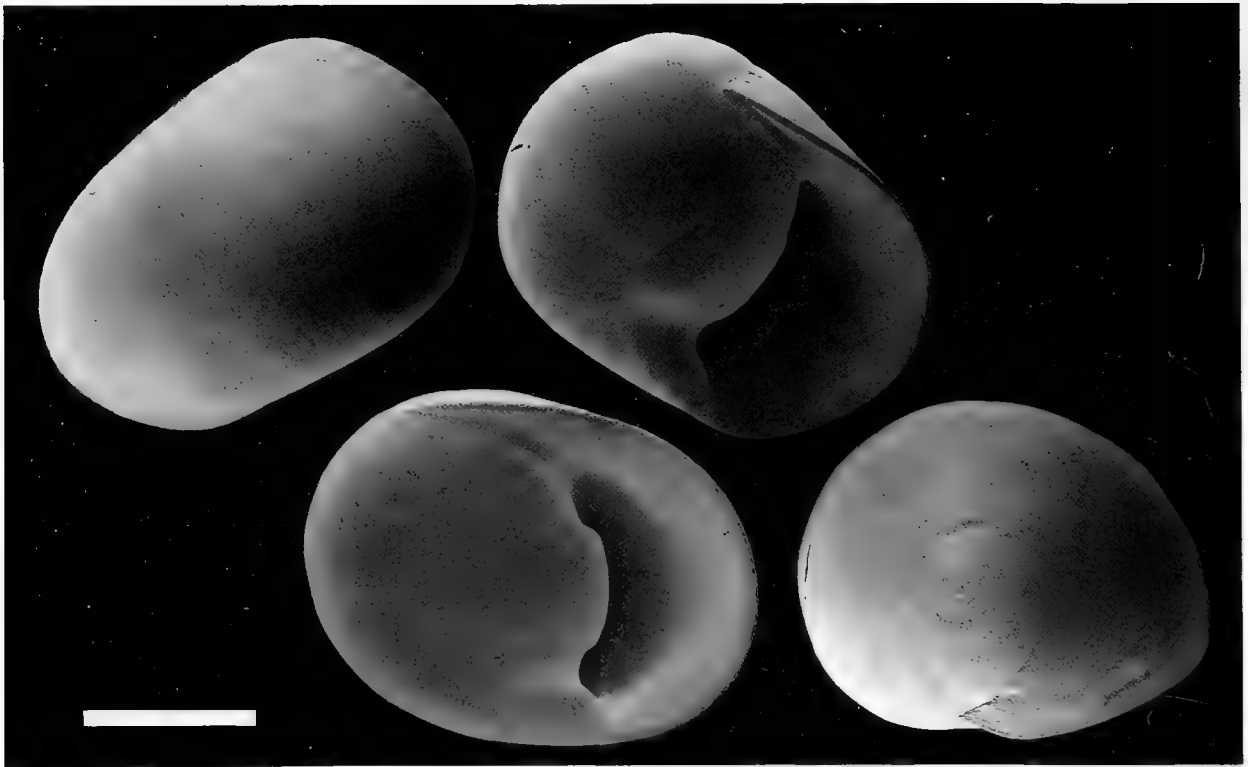


Figure 1. *Pisulina adamsiana* Nevill and Nevill, 1869 from Sipadan Island, Sabah, Malaysia (NSMT-Mo71619). Scale bar = 2 mm.

post-embryonic shells in *Smaragdia*. However, they did not elaborate on the systematic position of this enigmatic genus from their observations, and the systematic position of *Pisulina* has remained speculative.

Since 1989, the junior author and his co-workers have been conducting biological sampling in shallow-water submarine caves on tropical and subtropical Pacific islands with the help of skilled SCUBA divers. During the course of the sampling, they have found a molluscan community that is distinctive in species composition and reproductive biology (Kase and Hayami, 1992; Hayami and Kase, 1993, 1996). They also found that a huge number of empty shells of *Pisulina* species had accumulated in the bottom sediments in many caves, and that living animals were abundant on the walls and ceilings of several caves in Hawaii, Saipan, Palau, the Philippines and Malaysia.

The purpose of this paper is (1) to describe the conchological characteristics of *Pisulina* in detail, (2) to define the genus and discuss its systematic position based on conchological characteristics, (3) to review all previously known species of *Pisulina*, and (4) to describe new species.

Materials and methods

We examined more than 5000 empty shells of *Pisulina* species obtained from the bottom sediments of more than 50 submarine caves, tunnels, grottos or caverns (at depths

ranging from 1.3 to 55 m), on tropical and subtropical Pacific islands. We also examined shells in beach drift and dredged samples, and fossil shells from Henderson Island (the Pitcairn Group) and Niue Island (Cook Islands). In the descriptions given below, the "Material examined" headings refer to empty shells, unless otherwise stated. Living animals were obtained from walls inside caves and tunnels by hand, or by brushing the undersurface of coral rubble on the bottom sediments. Empty shells were obtained from the sediments (mainly calcareous mud) of the cave floors by hand sorting.

For comparison, we examined embryonic shells of *Neritilia rubida* (Pease, 1865) from Tahiti. In addition, live specimens of another *Neritilia* species [collected in a stream in Tabaru Valley, Yonaguni Island, Okinawa Prefecture, Japan; identified by Kubo and Koike (1992) as *N. rubida*] were kept in a freshwater aquarium, and embryonic shells were obtained after spontaneous oviposition and following development. In the aquarium, egg capsules which each retained only one embryo were laid in small pits on the undersurface of limestone cobbles taken from the original habitat. The veligers were hatched as embryonic shells after two weeks of oviposition.

We prepared specimens for SEM observation using standard techniques: shells were cleaned with an ultrasonic cleaner, dried, mounted on stages, coated with gold, and examined under a scanning electron microscope (JOEL T330A), or were examined in a low-vacuum mode without a

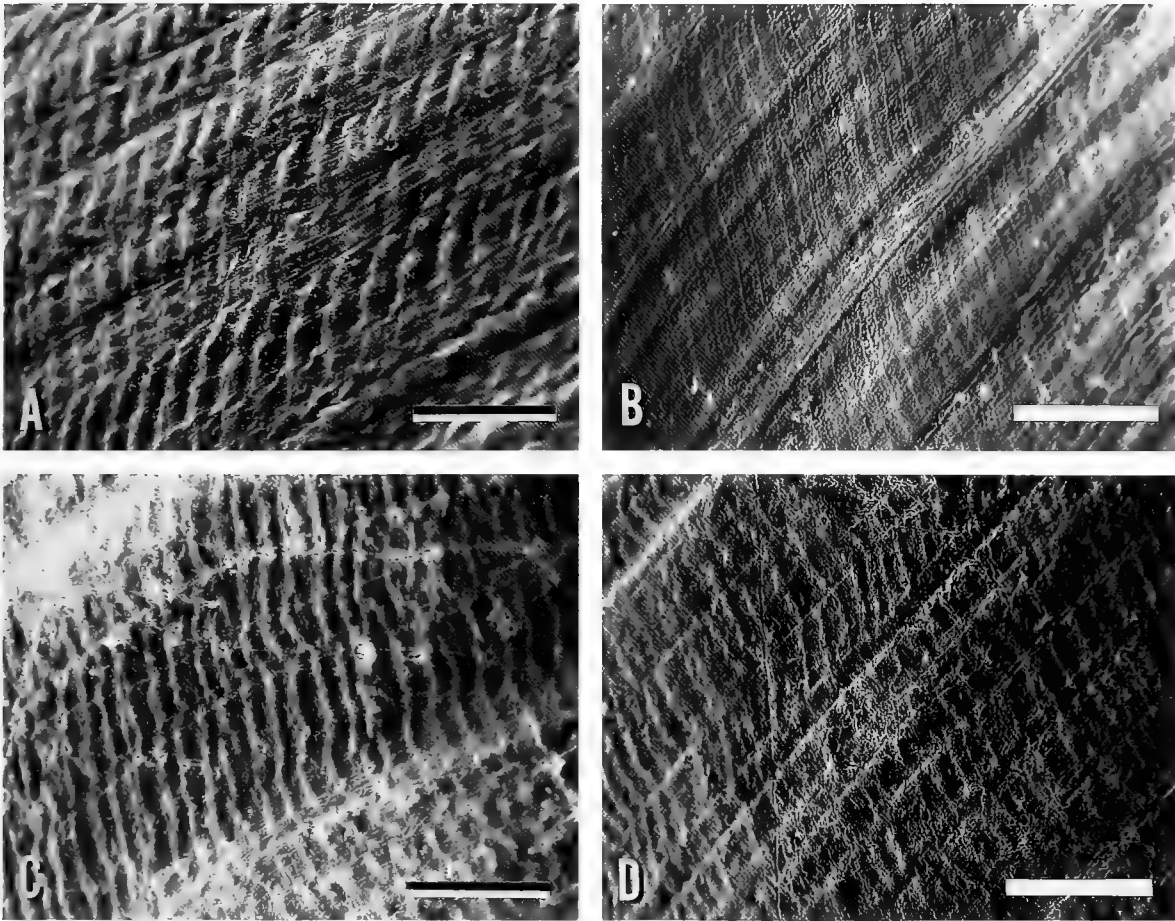


Figure 2. SEM micrographs of the subsutural surface of the last teleoconch whorls in four modern *Pisulina* species; all are oblique apical views. Scale bars = 50 μ m. **A.** *Pisulina adamsiana* Nevill and Nevill from Sipadan Island, Malaysia. **B.** *Pisulina biplicata* Thiele from Shimoji Island, Okinawa, Japan. **C.** *Pisulina maxima* sp. nov. from Sipadan Island. **D.** *Pisulina tenuis* sp. nov. from Yonaguni Island, Okinawa.

metal coating in another SEM (JEOL 5200LV). Polished and etched sections were prepared for microstructural analysis of the shell wall in the following manner: blocks of shells were embedded in synthetic resin, polished, cleaned ultrasonically to remove polishing grit, etched in 0.3% acetic acid for 60 seconds, and cleaned again. The terminology and usage of shell ultrastructure follow Carter and Clark (1985).

Museum abbreviations. — AMS: Australian Museum, Sydney; MNHB: Museum für Naturkunde der Humboldt-Universität, Berlin; MNHN: Muséum National d'Histoire Naturelle, Paris; NSMT: National Science Museum, Tokyo; UMZC: University Museum of Zoology, Cambridge, England; USNM: National Museum of Natural History, Washington.

Systematic description

Superorder Neritopsina Cox and Knight, 1960
Family Neritiliidae Schepman, 1908

Genus ***Pisulina*** Nevill and Nevill, 1869

Pisulina Nevill and Nevill, 1869, p. 160.

Type species. — *Pisulina adamsiana* Nevill and Nevill, 1869, by monotypy.

Distribution and age. — Tropical and subtropical Indo-Pacific. Late Miocene to Recent.

Diagnosis. — Shell small to medium in size, globose neritiform, white, smooth, solid. Inner lip of aperture smooth, convex, covered with a thick and widespread callus, with a robust projection or 3 to 7 teeth on margin. Outer lip with a weak inner ridge inside and a sharp margin. Protoconch either multispiral or paucispiral; multispiral

protoconch with a larval shell inclined approximately 30° to teleoconch axis, sculptured with several spiral ridges, and embryonic shell partially covered by larval shell whorls and also by first teleoconch whorl due to protoconch inclination. Outer layer of shell wall very thin, simple prismatic structure; each prism almost perpendicularly arranged to the outer shell surface. Operculum semicircular, paucispiral, thin, concave externally; external surface smooth, corneous, reddish straw in color; inner surface calcified except for marginal area, with an apophysis near base of inner margin.

General conchological features

Teleoconch.—The shell is small to medium in size, globose to subglobose or sometimes hemispherical, solid, white, and translucent when it is fresh (Figure 1). The teleoconch coils number less than four, increase rapidly in size, and have a less convex upper whorl surface. The suture is shallowly impressed. The last whorl is well inflated and has a round periphery. The exterior surface bears microscopic spiral ridges and very fine growth lines (Figure 2A–D). The aperture is small to large and crescent-shaped to semicircular in outline. The outer lip is prosocline, angled 30° to 50° from the shell axis, sharp along its margin, and is thickened interiorly into an indistinct inner ridge. The inner lip is covered with a smooth, thick and convex callus that spreads widely onto the base of the previous whorl. The adaxial margin of the inner lip bears a robust projection in *P. adamsiana* and *P. subpacificae*, and three to seven teeth in all other species. The inner line of the callus surrounds the columellar area, then merges gradually with the basal lip. The inner walls of the whorls are resorbed, producing a hollow cavity inside (Figure 3), except for the last 1/3 whorl, where the cavity forms a relatively long, narrow, tube-like inner space and continues to the apertural opening. Inside the whorls is a funnel-like cavity which is separated from the main cavity by a steep wall and positioned just beneath the inner lip callus. This cavity, visible from the outside through the translucent inner lip callus, encases the distal end of an adapically projected digestive gland. Two muscle attachment scars are carved as shallow depressions; one corresponds to the left shell muscle of the animal, is spirally elongate and located beneath the convex part of the inner line of the aperture, while the other corresponds to the right shell muscle, is subcircular in shape and located close to the apex.

Protoconch.—The protoconch is deeply immersed in the first teleoconch whorl, separated from the teleoconch by a clear line of demarcation, and is either multispiral or paucispiral (Figures 4A–F; 5A–E). A multispiral protoconch,

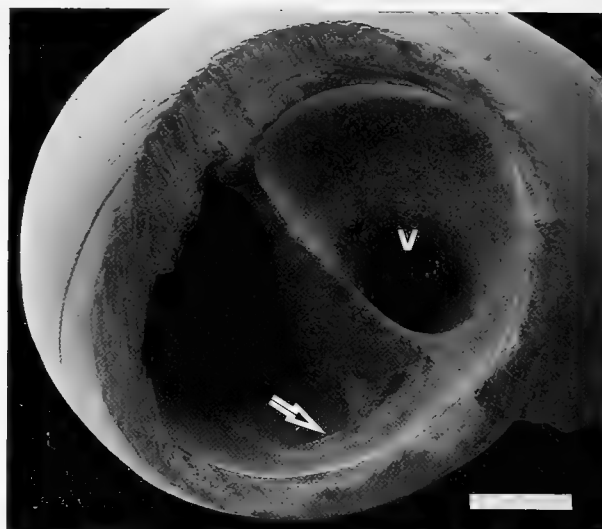
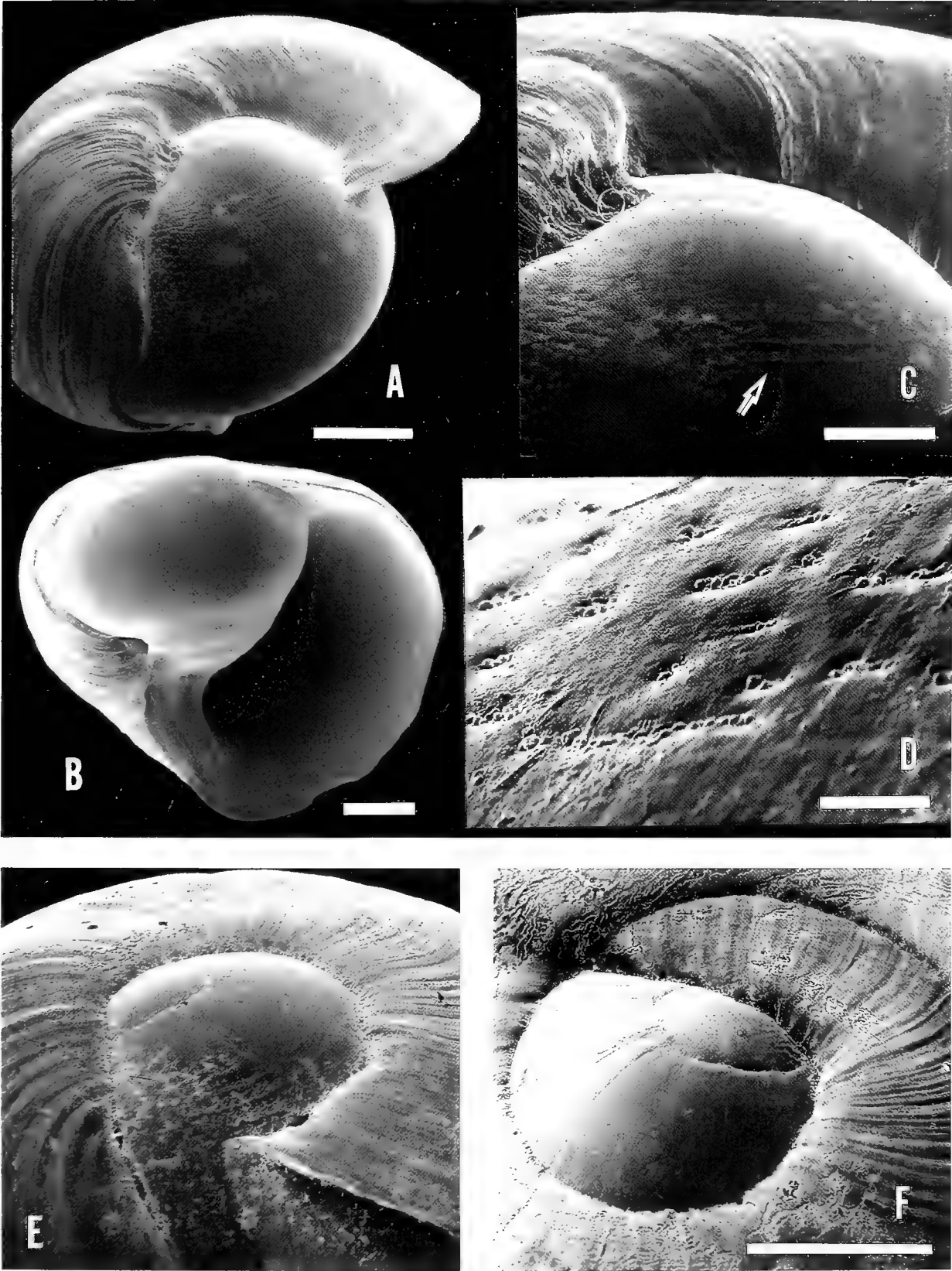


Figure 3. Shell (apical whorls removed) of *Pisulina adamsiana* Nevill and Nevill from South Kona, Hawai'i Island, showing the hollow internal space and the vertical cavity (v), the latter encasing the digestive gland of the animal; oblique apical view. Arrow indicates the elongate left muscle scar. Scale bar = 500 μm .

seen in *P. adamsiana* and *P. subpacificae*, consists of an embryonic shell (protoconch-I) and larval shell (protoconch-II). The embryonic shell is generally smooth and largely involved with the larval shell that bears four or five spiral ridges and many minute pits. The axis of the multispiral protoconch is sharply inclined (approximately 30°) compared to the teleoconch whorls, so the embryonic shell is partly covered by the initial teleoconch whorl (Figure 4A, E, F). The inner walls of the protoconch are resorbed into the teleoconch. A paucispiral protoconch, seen in some species, consists only of a large and smooth embryonic shell. In this case, the coiling axis of the protoconch appears to be the same as that of the teleoconch.

Shell microstructure.—The shell consists of three layers, excluding the myostracum, and Figure 7 shows their occurrence in the shell. The outermost layer (OL) is very thin (less than 20 μm thick in *P. adamsiana*), and is composed of simple, irregular prisms (Figure 6A, B). Each prism is less than 2 μm long, 0.3 μm thick, and oriented with its long axis less than 10° to the outer shell surface. The middle layer (ML) is of very thick, simple crossed-lamellar structure (Figure 6A–D). The inner shell layer (IL) consists of alter-

Figure 4. SEM micrographs of the multispiral protoconch in *Pisulina adamsiana* Nevill and Nevill. All specimens came from off South Kona, Hawai'i Island. **A–D.** Juvenile specimen with 0.6 of a teleoconch whorl. **A.** Abapertural view showing the biconvex and opisthocline larval shell aperture. Scale bar = 100 μm . **B.** Apertural view. Scale bar = 100 μm . **C.** Detail of the apical area of the protoconch, oblique lateral view. Embryonic shell partly exposed. Arrow indicates spiral ridges on the shoulder of the larval shell. Scale bar = 50 μm . **D.** Close-up of the larval shell surface near the aperture, showing the presence of granules within pits. Scale bar = 5 μm . **E.** Oblique apical view of a juvenile specimen with 0.9 of a teleoconch whorl, showing faint spiral ridges on the larval shell surface. Scale bar = 100 μm . **F.** Oblique apical view of an immature shell with 1.7 teleoconch whorls, showing wavy ridges on the embryonic shell surface that are visible due to a lesser degree of overlapping by the teleoconch whorl. Scale bar = 100 μm .



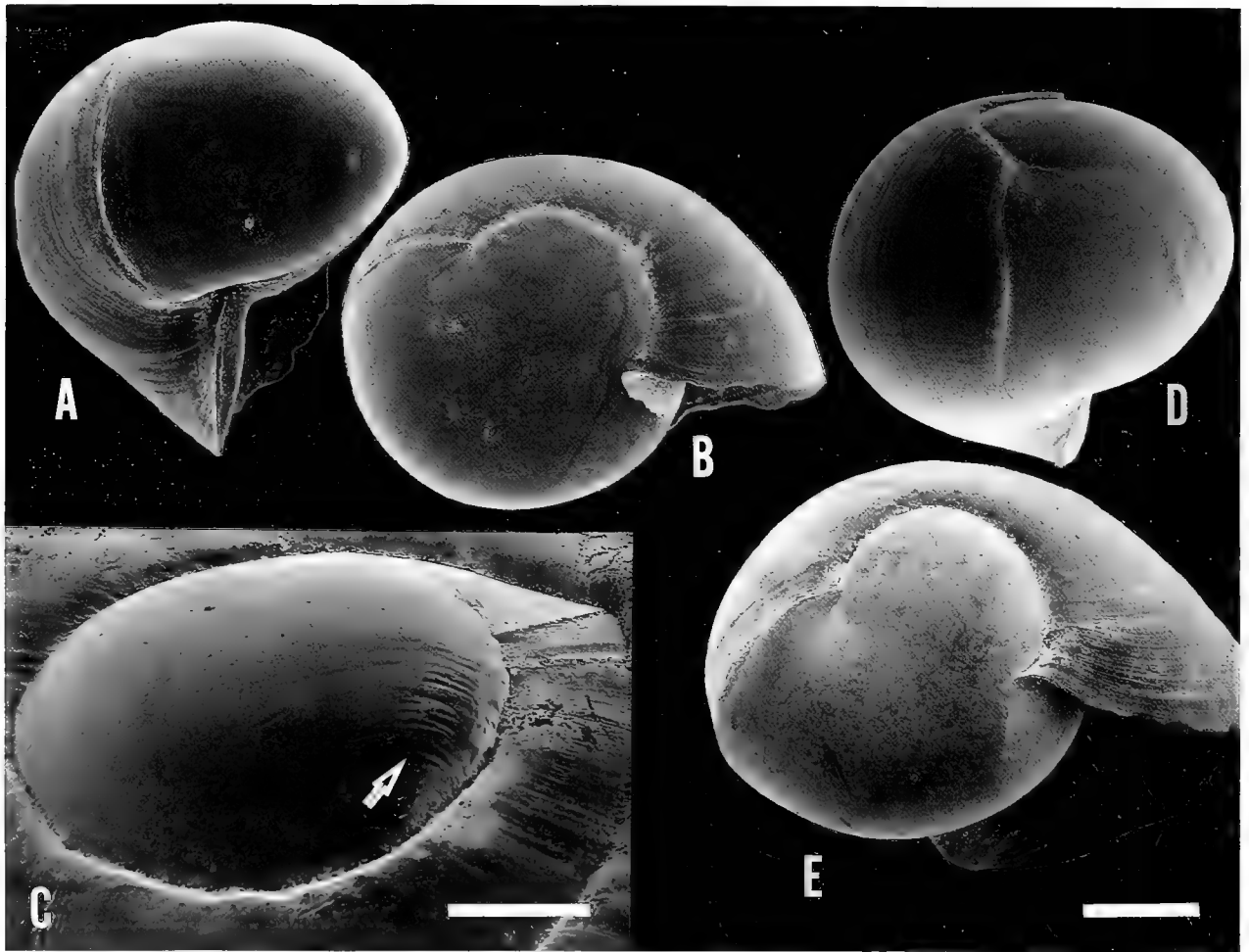
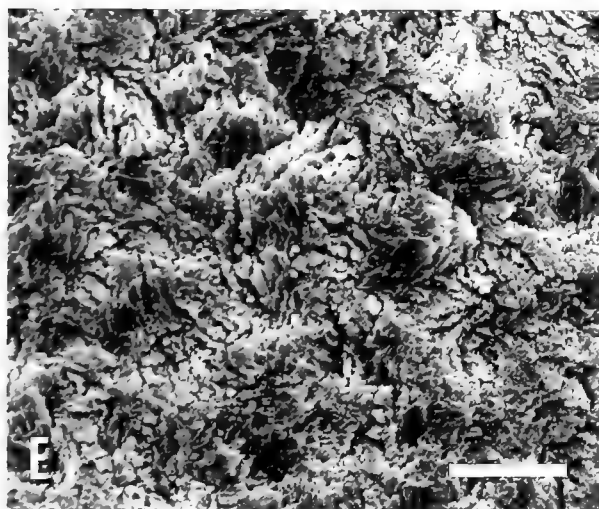
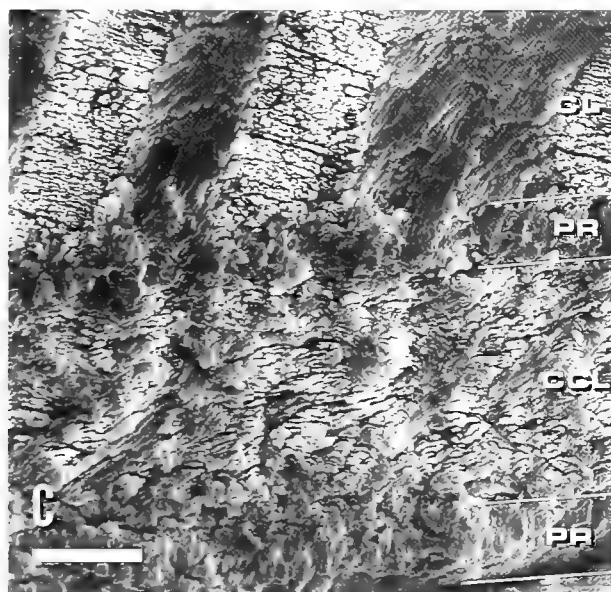
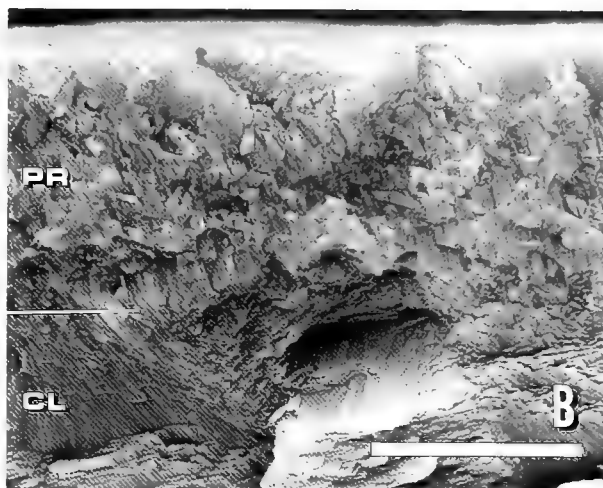
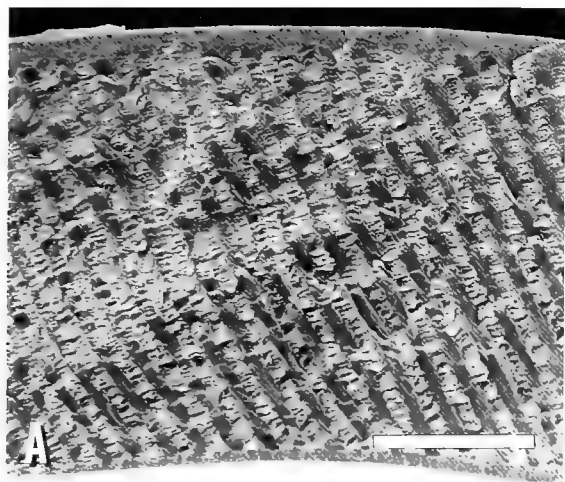


Figure 5. SEM micrographs of paucispiral protoconchs in *Pisulina* species. **A, B.** *Pisulina biplicata* Thiele, juvenile specimen with 0.5 of a whorl from off Kohama Island, Okinawa. Scale bar = 100 µm. **A.** Abapertural view. **B.** Slightly oblique apical view. **C.** *Pisulina maxima* sp. nov., oblique apical view of an immature specimen from off Aulong Island, Rock Islands, Palau. Arrow indicates longitudinal folds on the protoconch near the suture with the first teleoconch whorl. Scale bar = 50 µm. **D, E.** *Pisulina tenuis* sp. nov., juvenile specimens with 0.5 and 0.6 of a teleoconch whorl, respectively, from Yonaguni Island, Okinawa. Scale bar = 100 µm. **D.** Abapertural view showing transverse growth ridges near the protoconch aperture. **E.** Slightly oblique apical view.

Figure 6. SEM micrographs showing microstructures of the shell and operculum in *Pisulina adamsiana* Nevill and Nevill. **A.** Fractured shell surface of the outer lip of the aperture, cut perpendicular to the apertural margin, showing very thin outer prismatic layer and thick simple crossed-lamellar middle layer. The shell margin is to the right and the shell surface toward the top. Scale bar = 100 µm. **B.** Close-up of the fractured shell surface near the outer shell surface in **A**, showing details of the outer prismatic layer (PR) and the middle crossed-lamellar layer (CL). Scale bar = 10 µm. **C–E.** Etched surfaces of the section shown in Figure 7. **C.** The etched surface of an abapertural shell area, showing simple crossed-lamellar middle layer (CL) and inner layer. The inner shell surface faces toward the bottom. The inner layer consists of two irregular prismatic sublayers (PR) and an intervening complex crossed-lamellar layer (CCL). Scale bar = 10 µm. **D.** An etched shell surface near the back of the inner line of the inner lip shows the simple crossed-lamellar middle layer (CL) and the inner layer. The inner layer consists of alternating irregular prismatic sublayers (PR) and complex crossed-lamellar sublayers (CCL). Scale bar = 20 µm. **E.** Complex crossed-lamellar structure of the reconstructed inner shell wall. Scale bar = 10 µm. **F.** Fractured surface of an operculum, showing spherulitic prismatic structure. Scale bar = 10 µm.



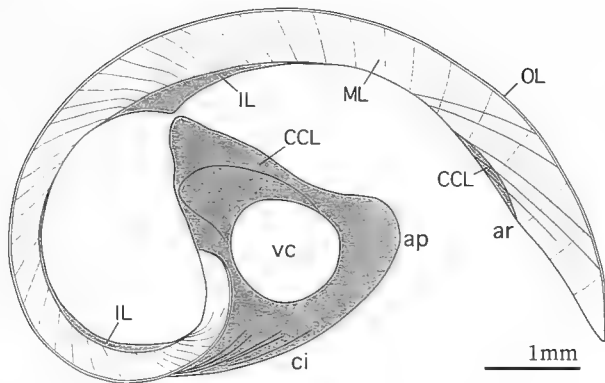


Figure 7. Arrangement of shell layers in *Pisulina adamsiana* Nevill and Nevill. The section is roughly perpendicular to the shell axis. Abbreviations: OL: very thin outer layer with prismatic structure; ML (light gray): thick middle layer with simple crossed-lamellar structure; IL (dark gray): inner layer made up of alternating sublayer(s) of complex crossed-lamellar and simple prismatic structures; CCL (dark gray): complex crossed-lamellar structure; ap: apertural projection; ar: apertural ridge; ci: callused inner lip of aperture; vc: vertical cavity.

nating sublayer(s) of complex crossed-lamellar and simple prismatic structure (Figure 6C, D). The prismatic sublayers consist of irregular prisms that are arranged vertically. The first-order lamellae of the complex crossed-lamellar structure are indistinct, variable in shape, and composed of a small number of thin, lath-like second-order lamellae (Figure 6E). The same shell structure is present in the robust inner lip area and in a small area just posterior to the inner ridge of the aperture, which are areas constructed secondarily after absorption of the original layers (CCL in Figure 7).

Operculum.—The operculum is semicircular in shape, with a minimum length/maximum length ratio of ca. 0.7, paucispiral, rather thin, and has a concave exterior surface (Figures 8A, B; 9A–C). The exterior surface fits well into the convex surface of the shell's inner lip when the animal fully extends its head-foot mass. The number of volutions may be up to 1.7, apart from the nucleus. The operculum consists of an outer corneous layer (up to 5 μm thick) and inner calcareous layers. The surface of the outer corneous layer is smooth (except for faint growth lines), reddish straw in color, and the color gradually becomes paler from the margin to nucleus. The nucleus appears only on the outer surface, is semicircular, located more or less abaxially and adapically from the center, paucispiral in *P. adamsiana* (Figure 8B) and concentric in the other modern species (Figure 9C). The inner surface of the operculum is calcified, except for the marginal area. The calcified area is covered with fine growth lines and bears a long apophysis near the base of the inner margin. The apophysis appears first as a weak ridge along the opercular suture, then becomes a curved calcified rod, and finally projects beyond the margin while remaining attached along its whole length to the basal margin of the operculum by a thin septum-like base. The muscle attachment scar can be divided into three areas: two are shallow, elongate depressions that are positioned at the

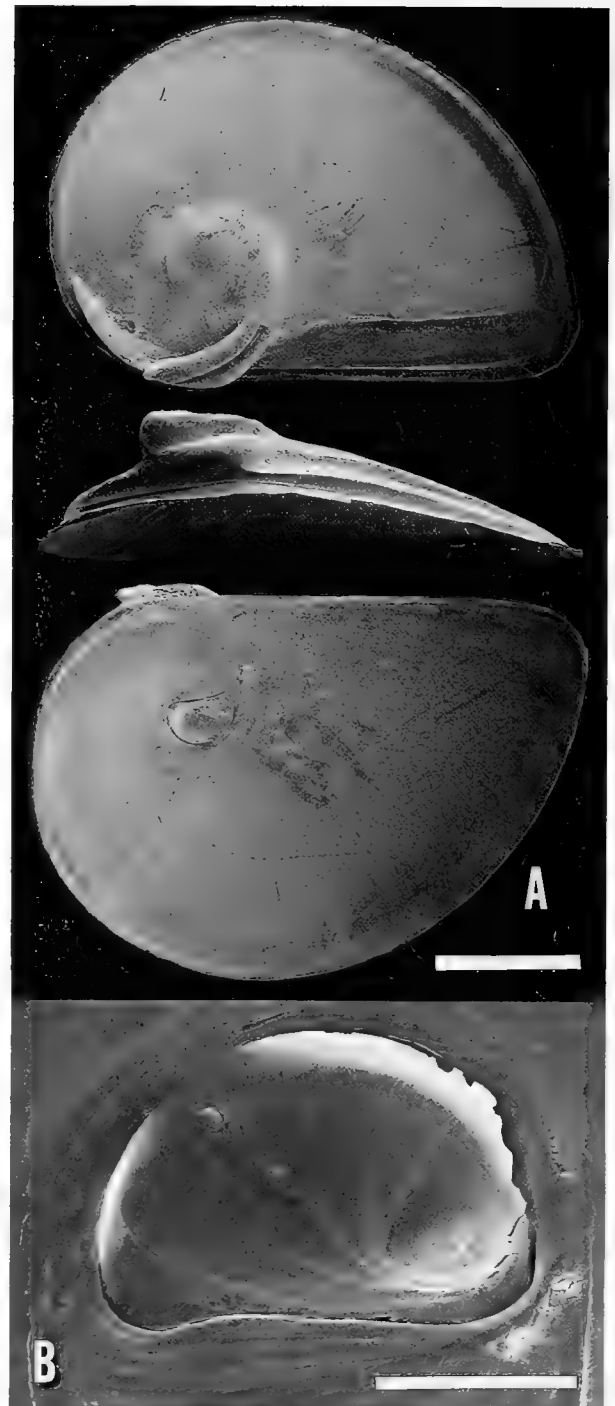


Figure 8. Operculum of *Pisulina adamsiana* Nevill and Nevill from Sipadan Island, Malaysia. **A.** Internal, lateral and external views (arranged from top to bottom). Scale bar = 500 μm . **B.** Oblique lateral view of the paucispiral nucleus on the external surface, showing 0.3 of a volution. Scale bar = 100 μm .

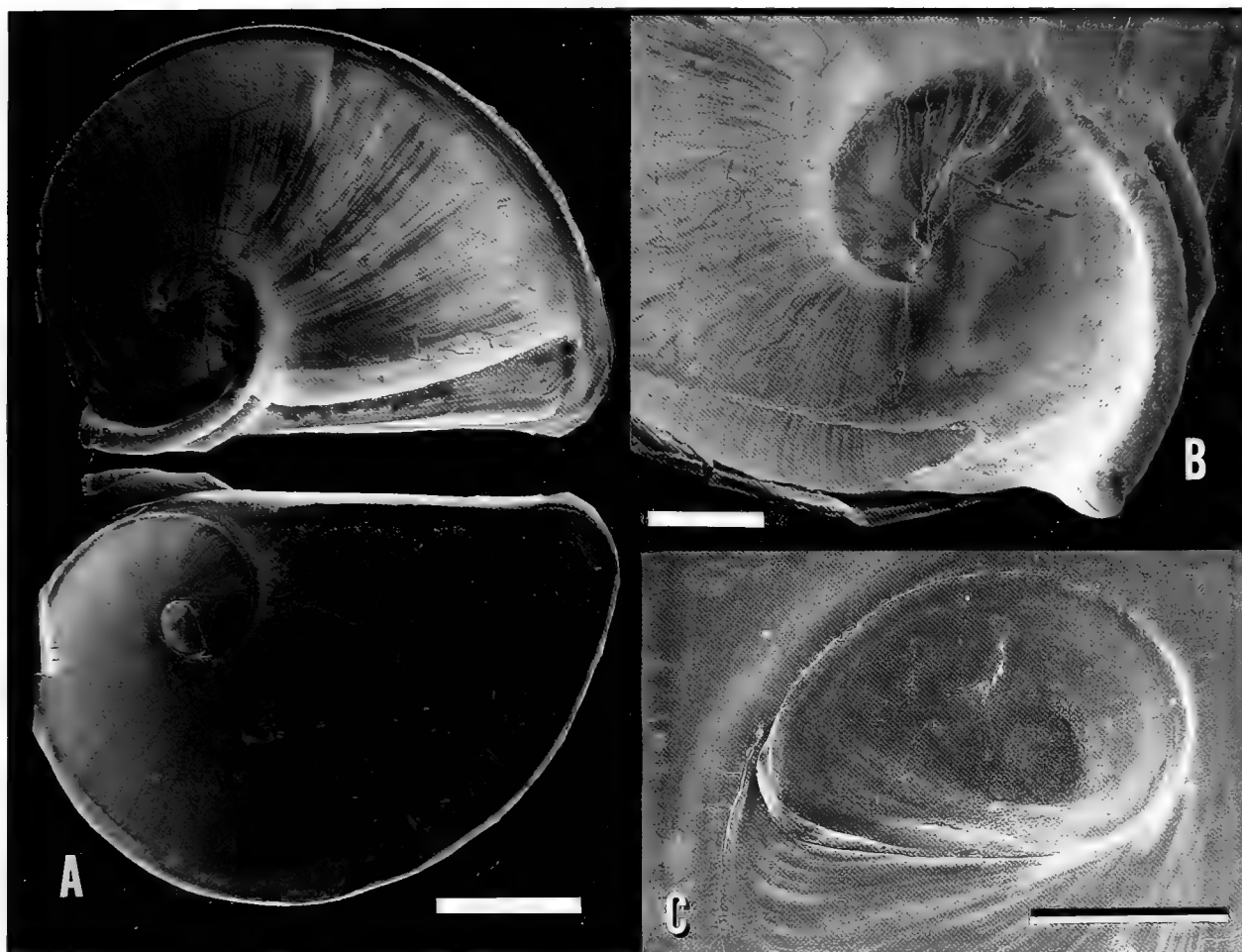


Figure 9. Operculum of *Pisulina maxima* sp. nov. from Sipadan Island, Malaysia. **A.** Internal (top) and external (bottom) views. Scale bar = 500 µm. **B.** Detail of apophysis and muscle attachments on the internal surface. Scale bar = 200 µm. **C.** Oblique view of the concentrically growing nucleus on the external surface of operculum. Scale bar = 100 µm.

inner and basal margins, and the other is between the apophysis and nucleus and is thicker than the other calcified areas due to having additional calcitic layers (Figure 9B). The calcareous part of the operculum is composed of spherulitic prisms (Figure 6F).

Systematic position of *Pisulina*

The protoconch morphology and shell microstructure of *Pisulina* are unique and almost identical to those of the freshwater genus of Neritopsina, *Neritilia* Martens, 1879; these are the only conchological characters useful for systematic placement.

Apart from species with non-planktotrophic development (see below), protoconchs of extant aquatic members of Neritopsina are quite uniform in shape and differ from those of all other gastropods (Bandel, 1982; Sasaki, 1998). The protoconchs of the following genera have been figured previ-

ously as SEM images: *Nerita* (Bandel, 1982; Sasaki, 1998), *Smaragdia* (Robertson, 1971; Bandel, 1982; Herbert and Kilburn, 1991), *Clithon*, *Neritina*, *Septaria* (Bandel and Riedel, 1998) [Neritidae]; *Phenacolepas* (Bandel, 1982; Sasaki, 1998), *Shinkailepas*, *Olgasolaris* (Beck, 1992) [Phenacolepadidae] and *Neritopsis* (Bandel and Frýda, 1999) [Neritopsidae]. These genera all share the same protoconch features: the embryonic shell is globular in shape, and the larval shell is oval to globular naticiform and has less than 3.5 volutions. As Bandel (1982) has noted, the larval shell is smooth except for fine growth lines, coils almost planispirally, and the suture line abuts the surface more adapical to the previous suture, so that the number of coils cannot be counted from the outside. Moreover, the inner walls of the larval shell are absorbed internally (*Neritopsis* is a possible exception; Bandel, 1992).

The protoconch of *Pisulina adamsiana* is fundamentally the same as in the Neritopsina mentioned above. However,

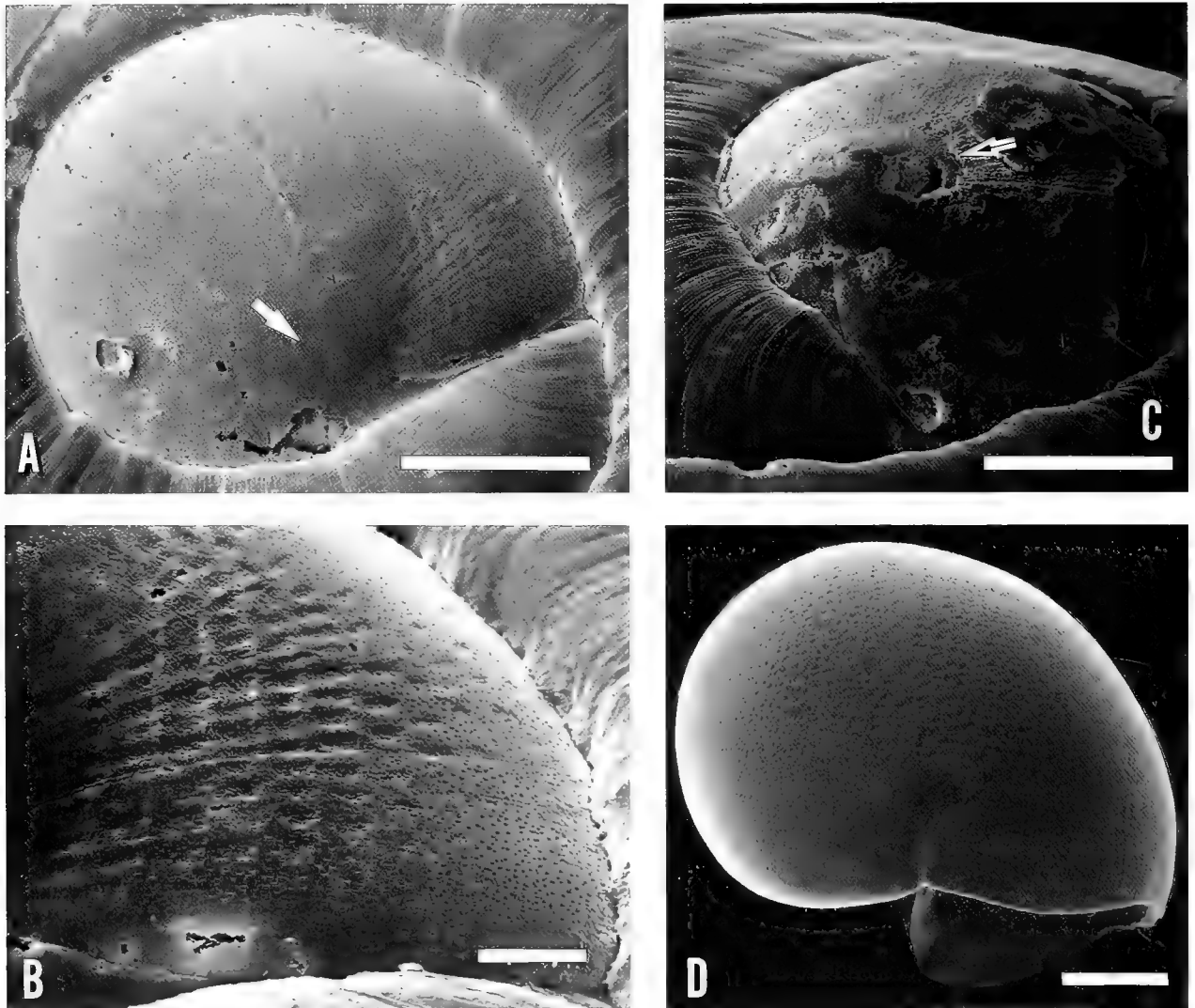


Figure 10. Multispiral protoconch and embryonic shell of *Neritilia*. **A C.** Immature shells of *Neritilia rubida* (Pease) from Tahiti. **A.** Apical view of a juvenile shell with 1.2 teleoconch whorls. The surface is mostly intact. Arrow indicates the apex of the larval shell. Scale bar = 100 μm . **B.** Oblique close-up of the larval shell surface in A, showing the presence of spiral and axial ridges and minute pits entirely covering the protoconch surface. Scale bar = 20 μm . **C.** Oblique apertural view of juvenile shell with 1.2 teleoconch whorls. Outermost layer of the protoconch is partially eroded, so that the suture and growth lines of the larval shell are visible. Arrow indicates suture line. Scale bar = 100 μm . **D.** Apical view showing an embryonic shell of *Neritilia* sp. that was extracted from an egg capsule shortly before hatching. Part of the operculum protrudes from the aperture. Scale bar = 20 μm .

as already pointed out by Herbert and Kilburn (1991), the larval shell of *P. adamsiana* is distinctly tilted with respect to the teleoconch (Figure 4A–F). This tilting resulted from the change in direction of the growth lines from the larval shell (opisthocline) and the teleoconch whorls (prosocline). In addition, *P. adamsiana* has characteristic ridges (Figure 4A, C, E) and microscopic pits (Figure 4C, D) on the larval shell surface near the aperture (see description of *P. adamsiana*, below), which are sculptural features unknown in the other aquatic groups of Neritopsina.

We have found that members of the freshwater and brackish-water genus *Neritilia* have a protoconch almost identical to that of *P. adamsiana*, suggesting a close affinity between the two genera. Bandel and Riedel (1998) have already noted the unique protoconch morphology of *Neritilia* within the superfamily Neritoidea. The protoconch surface of the type species, *Neritilia rubida*, is smooth and has no suture line, so it appears to be a simple globular protoconch (Figure 10A, B). However, this is due to the subsequent laying down of a very thin calcareous layer over the surface of a



Figure 11. Oblique lateral view of a paucispiral nucleus with 0.3 of a volution on the operculum of *Neritilia* sp. from Yonaguni Island, Okinawa. Scale bar = 50 μ m.

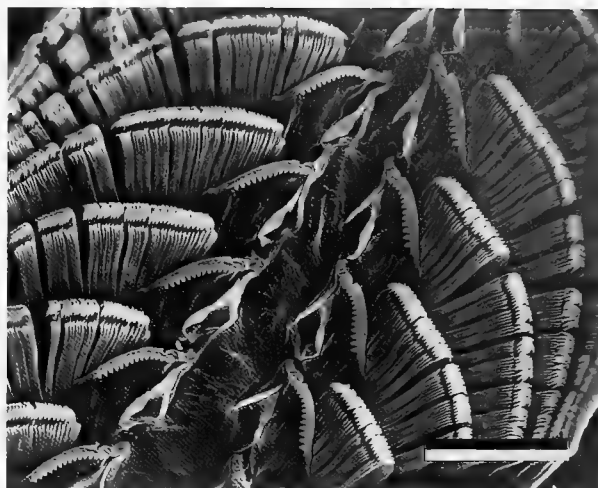


Figure 12. Radula of *Pisulina maxima* sp. nov. from Sipadan Island, Malaysia. The radula is characterized by a large, strongly oblique outer lateral tooth and the absence of a central tooth, the features almost identical to that of *Neritilia* (see Baker, 1923). Scale bar = 50 μ m.

multispiral protoconch. In specimens whose protoconch surfaces are slightly eroded, the suture line and distinct growth lines are visible (Figure 10C), the once-hidden embryonic shell emerges close to the suture of the teleoconch, and a discontinuity in coiling is noticeable between the larval shell and teleoconch. The number of larval shell coils cannot be precisely counted, but appears to be about one, as seen in *P. adamsiana* (the paucispiral nucleus of the operculum, which is formed during the larval phase, is also similar to that of *P. adamsiana* in number of volutions; Figure 11). The calcareous layer over the protoconch appears to have been secreted after the last whorl of the larval shell was formed. In addition to the presence of this calcareous layer, *N. rubida* shows additional minor differences in its protoconch: the inclination of the coiling axis appears to be somewhat smaller, the larval shell has more numerous spiral ridges (five or six; Figure 10B) than *P. adamsiana*, and the microscopic pits are scattered all over the surface of both embryonic and larval shells without an evident pattern (Figure 10B, D). Bandel and Riedel (1998, fig. 6A, B) figured the protoconch of *Neritilia* sp. cf. *N. rubida*, from the Matutinao River, Cebu, the Philippines. The spirally arranged pits on the larval shell of this species differ from those described here for *N. rubida*. The spiral rows of pits in the Philippine *Neritilia* species evidently are a homologous character shared with *P. adamsiana*.

Shell microstructure is a second clue to the close relationship between *Pisulina* and *Neritilia*. Previous descriptions of shell microstructure of Neritopsina have been mostly restricted to Neritidae (e.g., Bøggild, 1930; Gainey and Wise, 1980; Bandel, 1990). The presence of a calcitic outer layer (with a homogeneous or prismatic structure) and aragonitic middle and inner layers (crossed-lamellar structure) are features shared among Neritopsina (e.g., Ponder and Lindberg, 1997:103). *Pisulina* has shell microstructure features that are basically the same as seen in Neritidae (Figures 6A–E;

7). However, *Pisulina* differs markedly from Neritidae in the inclination of prisms in the outer layer. The prisms are arranged almost perpendicularly in *Pisulina* (Figure 6B), while they are almost horizontal or very oblique relative to the exterior shell surface in neritids (Bøggild, 1930; Knight *et al.*, 1960:123; Bandel, 1990; personal observation). Although the outer prismatic layer is brown in color and much thicker than in *Pisulina*, *Neritilia rubida* shares characteristic features regarding the inclination and size of prisms with *Pisulina*.

The monogeneric family Neritiliidae was erected for the genus *Neritilia* by Schepman (1908) based upon its unique radular morphology. However, the genus has been assigned to the subfamily Neritiliinae of Neritidae (e.g., Baker, 1923; Thiele, 1929; Wenz, 1938; Knight *et al.*, 1960). Holthuis (1995) has recently shown the paraphyly of "Neritidae" and concluded that *Neritilia* is the sister group of Neritidae and Phenacolepadidae. Thus, *Neritilia* should be classified as an independent family of the superorder Neritopsina, namely Neritiliidae Schepman, 1908, rather than being placed in Neritidae.

Although the detailed systematic position of *Pisulina* must ultimately be determined by phylogenetic analysis based on conchological, anatomical, and molecular criteria, it is reasonable to conclude at present that *Pisulina* is not a member of Neritidae, but should be allocated along with *Neritilia* to Neritiliidae. The close relationship between the two genera is also confirmed by radular and anatomical characters (Figure 12; Kano and Kase, in preparation). We believe that the protoconch with the whorl inclination and spiral ridges, and the almost perpendicular prisms in the outer shell layer, are synapomorphies of *Pisulina* and *Neritilia*.

These synapomorphies are important criteria for re-

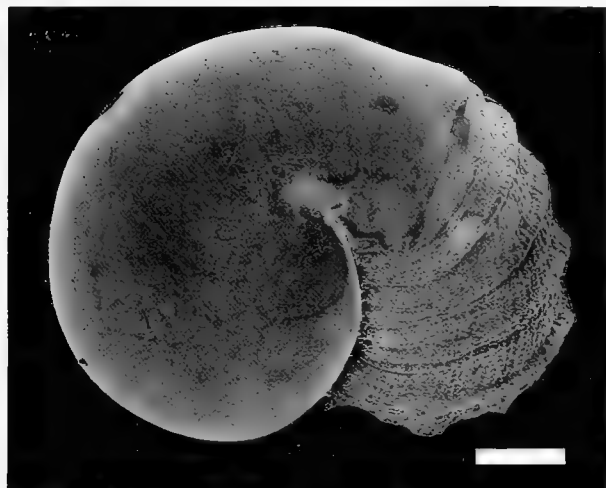


Figure 13. Paucispiral protoconch of *Neritopsis radula* (Linnaeus), juvenile specimen with 0.2 of a teleoconch whorl, from Yonaguni Island, Okinawa, in apical view. Bandel and Fryda (1999) illustrated a multispiral protoconch of *N. radula* from Mauritius. Further research is needed to resolve whether *N. radula* from the western Indian Ocean and Pacific are different species or an example of poecilogony (different early ontogenies within a single species; Bandel and Riedel, 1998), unknown among the Gastropoda. Scale bar = 100 μ m.

evaluating fossil species previously placed in Neritidae, which ranges in age from Triassic to Recent. Knight *et al.* (1960) recognized 19 fossil genera (4 are still living) in the family and diagnosed most genera solely on the basis of teleoconch characters. The apical whorls of fossil neritids tend to be lost by abrasion and/or dissolution, but in rare instances they are preserved intact in sediments deposited in low-energy, soft-bottom environments. By examining fossil species, we have found that two species, *Pisulinella miocenica* Kano and Kase, 2000, and "*Neritilia*" *tracyi* Ladd, 1965, both from the Miocene of the Marshall Islands, are undoubtedly members of Neritiliidae. As in *Neritilia* and *Pisulina*, these two species possess an inclined protoconch bearing spiral ridges, but differ from *Neritilia* and *Pisulina* in important ways (Kano and Kase, 2000; unpublished data).

Implications of paucispiral protoconch

Pisulina species have either a paucispiral or multispiral protoconch. Nevertheless, the species are undoubtedly closely related to one another, because of the many close similarities in other shell characters. We suggest that the paucispiral protoconch originated from the multispiral protoconch of an ancestral *Pisulina* species, as described below.

Most aquatic species of Neritopsina have a long planktotrophic duration after hatching from their egg capsule, and feeding veligers secrete a multispiral larval shell. However, species of some freshwater genera (e.g., *Theodoxus*) have a very large (ca. 0.9 mm) paucispiral protoconch and their development is quite different from that

of other members of Neritopsina. They undergo benthic development, and metamorphosis occurs within the egg capsule by means of nurse-egg feeding (Bandel, 1982). The juveniles crawl out from the capsule with their foot. According to Holthuis (1995), free-swimming veligers (ancestral for the group) were lost at least four times in the evolutionary history of Neritidae, and in *Nerita* and *Vitta* the loss occurred within the genus (or subgenus). The non-planktotrophic (benthic or lecithotrophic) development of *Pisulina* seems to have originated from a planktotrophic ancestor, after the origin of the genus, by exploiting an adaptive modification different from freshwater neritids. Benthic development is much more prevalent in freshwater invertebrates than in their marine relatives, because the downstream loss of freshwater larvae in moving water is the primary determinant for benthic development (Holthuis, 1995). Meanwhile, the non-planktotrophic development of *Pisulina* may be an adaptation to the unique cryptic environments in marine caves. Kase and Hayami (1992) and Hayami and Kase (1996) have shown that the predominance of non-planktotrophic development and the dominance of brooding species among submarine cave bivalves primarily resulted from an adaptation to food-limited conditions. Although no examples of this have been found in gastropods so far, it may be that *Pisulina* underwent non-planktotrophic development and acquired a paucispiral protoconch by adapting to a cryptic habitat. *Neritopsis radula* (Linnaeus, 1758), another cave-dwelling species of Neritopsina, developed a similar paucispiral protoconch (Figure 13).

It is worth noting that paucispiral and concentric opercular nuclei are connected with multispiral and paucispiral protoconchs. The paucispiral nucleus (the operculum of a veliger) grows during the planktotrophic period, while the concentric nucleus is formed in the egg capsule, providing an additional criterion for inferring the mode of development in gastropods.

Pisulina adamsiana Nevill and Nevill, 1869

Figures 1; 2A; 3–4; 6–8

Pisulina adamsiana Nevill and Nevill, 1869, p. 160, pl. 17, fig. 4; Thiele, 1925, p. 32, pl. 3, fig. 16; Thiele, 1929, p. 111, fig. 54; Wenz, 1938, p. 431, fig. 1060; Knight *et al.*, 1960, p. 285, fig. 185-3; Habe, 1963, p. 231, 232, fig. 1; Ladd, 1977, p. 14, 15, pl. 1, figs 1, 2; Herbert and Kilburn, 1991, p. 320–322, figs. 1–3; Hinoide and Habe, 1991, p. 49 (in part), fig. 1.

Material examined.—INDIA: "Calcutta"; 1 specimen, coll. Paetel, MNHB.—"Ganges River delta" (21°40'N, 88°00'E); pre 1913, 3 specimens, AMS C-034497. —MALDIVES: Ari Atoll; 25 m depth; January 1996; 1 specimen, coll. S. Gori. —JAPAN: "Shodokutsu (= small cave)", Ie Island, Okinawa (26°42.9'N, 127°50.1'E); 20 m depth, totally dark submarine cave; 1988; 12 specimens.—"Umagai" diving site, north of Hatenohama, east of Kume Island (26°21.1'N, 126°53.1'E); 24–28 m depth, submarine caves, totally dark inside; July 1996, 2 specimens.—"Witch's House (= Majono-yakata)" diving site, northwest of Shimoji Island, Miyako Islands, Okinawa (24°49.3'N, 125°08.3'E); 35 m depth, submarine

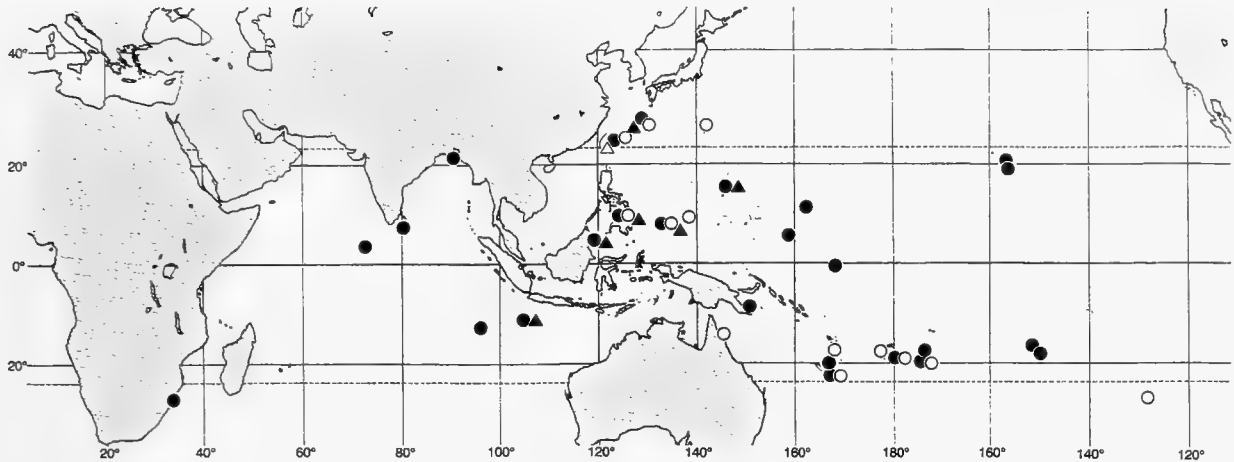


Figure 14. The geographic distribution of Recent *Pisulina* species. *Pisulina adamsiana* Nevill and Nevill (solid circles), *Pisulina biplicata* Thiele (open circles), *Pisulina maxima* sp. nov. (solid triangles) and *Pisulina tenuis* sp. nov. (open triangle). The type locality of *P. biplicata* is not plotted, because it was designated only as "Indian Ocean."

cave, totally dark inside; 54 specimens (10 specimens NSMT-Mo71618). — "Torike" diving site, northwest of Shimoji Island (24°49.1'N, 125°08.3'E); 12–40 m depth, several caves branching from a huge tunnel, gloomy to totally dark inside; 1992–1996, 2 specimens. — "Black Hole" diving site, northwest of Shimoji Island (24°49.1'N, 125°08.3'E); 35 m depth, submarine cave, totally dark inside; 1 specimen. — "Sabachi Cave", southeast of Yonaguni Island, Yaeyama Islands, Okinawa (24°26.1'N, 122°57.5'E); 25–30 m depth, submarine cave, totally dark inside; September 1994, 2 specimens. — MALAYSIA: "Turtle Cavern", Sipadan Island, west Celebes Sea, Sabah (5°04.8'N, 118°36.5'E); 9–17 m depth, totally dark inside; May 1997, 10 specimens (including 9 live individuals; 1 empty shell NSMT-Mo71619). — PHILIPPINES: "Marigondon Cave" diving site, Mactan Island, Cebu (10°15.8'N, 123°59.2'E); 27 m depth, large submarine cave, totally dark inside; May 1994, more than 1000 specimens; November 1998, 3 live specimens. — Balicasag Island, Panglao, Bohol (9°32.7'N, 123°40.7'E); 14–40 m depth; submarine caverns, gloomy inside; May 1994, 162 specimens (10 specimens NSMT-Mo71620). — "Mapatin Cave" diving site, southwest of Marican Island, Batangas, Luzon (13°40.0'N, 120°49.0'E); 46 m depth, lava tube, totally dark inside; November 1998, 1 live specimen. — PALAU: "Virgin Hole", west of Ngemelil Island, Rock Islands (7°07.3'N, 134°14.1'E); 17 m depth, submarine cave, totally dark inside; April 1995, 4 specimens. — "Siaes Tunnel" diving site, southwest of Siaes drop off, ca. 6 km west-northwest of Aulong Island, Rock Islands (7°18.7'N, 134°13.6'E); 24–53.5 m depth, huge submarine tunnel; April 1995, 141 specimens; December 1997, 19 specimens. — NORTHERN MARIANAS: near "Grotto" diving site, north of Saipan Island (15°15.3'N, 145°49.5'N); 12–30 m depth, huge cave, gloomy to totally dark inside; November 1997, 31 specimens (including 3 live individuals). — near "Tinian Grotto" diving site, west of Tinian Island; 50–51 m depth, huge cave, gloomy to totally dark; November 1997, 6 specimens. — POHNPEI: "Plang Point" diving site, west of Pohnpei Island (6°51.4'N, 158°

06.6'E); 55m depth, cavern, gloomy inside; November 1999, 2 specimens. — HAWAII: "Worm Cave", off Ahihi-Kinau, Makena, Maui Island (20°35.3'N, 156°25.8'W); 26–31 m depth, submarine cave, gloomy to totally dark inside; October 1997, 54 specimens (including 5 live individuals). — "Lost Crater Caves" diving site, off Ahihi-Kinau (20°35.3'N, 156°25.7'W); 25 m depth, submarine lava cave, gloomy inside; October 1997, 1 live individual. — "Long Lava Tube", off Pali Kaholo, South Kona, Hawai'i Island (19°21.8'N, 155°56.8'W); 11 m depth, long lava tunnel, gloomy; November 1997, 16 specimens. — "Gustav Cave", off Ka'u Loa Point, South Kona (19°19.1'N, 155°53.2'W); 6–8 m depth, submarine cave, gloomy to totally dark inside; November 1997, 19 live individuals. — PAPUA NEW GUINEA: between Magulata and Kabuluna Points, Kiriwina Island, Trobriand Group (8°27'S, 150°59'E); 73 m depth, coral sand bottom, outside outer reef; June 1970, 1 specimen, coll. W. F. Ponder and P. H. Colman, AMS C-345150. — NAURU: Aiwo (0°32.6'S, 166°54.5'E); 15–25.5 m depth, cavern, open to gloomy inside; November 1999, 43 specimens. — AUSTRALIA: "Hangover Cave" diving site, west of Direction Island, Cocos (Keeling) Islands (12°06.3'S, 96°52.5'E); 51–52.3 m depth, cavern, gloomy inside; December 1999, 4 specimens. — "Boat Cave" diving site, Christmas Island; 2.4 m depth; totally dark inside; November 1999, 1 specimen. — "Thunder Dome" diving site, Christmas Island; 7.7–10.2 m depth, long cave, totally dark inside; December 1999, 12 specimens. — NEW CALEDONIA: east of Nuu Poa islet, Iles des Pins, New Caledonia (22°31.6'S, 169°25.8'E); 17–19.5 m depth, meandering submarine cave, gloomy inside; October 1996, 3 specimens, MNHN. — FIJI: north of Ono Island, Great Astrolabe reef (18°51.8'S, 178°27.0'W); 7–16 m depth; submarine tunnel, gloomy inside; December 1996, 2 specimens. — northwest of Dravuni Island, Great Astrolabe reef (18°45.3'S, 178°28.0'W); 23–24 m depth; December 1996, 18 specimens. — TONGA: north of Haano Island, Ha'apai Group (19°38.2'S, 174°18.0'W); 44 m depth, cavern; December 1996, 6 specimens. — west of Mo'ung'one Island, Ha'apai

Table 1. Comparison of shell characters in five species of *Pisulina*. Some of the character states in *Pisulina subpacific* Ladd (those shown in parentheses) may not represent general features of the species, owing to the immature condition of the holotype.

| Species | Shell diameter of largest specimen | Shell thickness | Width of ridges on teleoconch surface | Apertural width | Number of inner lip teeth |
|---------------------------------|------------------------------------|-----------------|---------------------------------------|-----------------|---------------------------|
| <i>Pisulina adamsiana</i> | 6.7 mm | thick | ca. 7 μ m | small | 1 |
| <i>Pisulina subpacific</i> | (1.2 mm) | thick | ? | small | 1 |
| <i>Pisulina biplicata</i> | 4.8 mm | thick | ca. 1 μ m | small | 3–5 |
| <i>Pisulina maxima</i> sp. nov. | 13.7 mm | very thick | ca. 4 μ m | very large | 3–7 |
| <i>Pisulina tenuis</i> sp. nov. | 4.0 mm | thin | ca. 4 μ m | large | 4–5 |

| Species | Sinuation of inner line near base | Tubercle on basal lip | Protoconch coiling | Max. dimension of protoconch exposed above teleconch |
|---------------------------------|-----------------------------------|-----------------------|--------------------|--|
| <i>Pisulina adamsiana</i> | absent | present | multispiral | 155–215 μ m |
| <i>Pisulina subpacific</i> | absent | (absent) | multispiral | 275 μ m |
| <i>Pisulina biplicata</i> | present | absent | paucispiral | 155–220 μ m |
| <i>Pisulina maxima</i> sp. nov. | present | absent | paucispiral | 180–275 μ m |
| <i>Pisulina tenuis</i> sp. nov. | present | absent | paucispiral | 210–300 μ m |

Group (19°23.2'S, 174°28.6'W); 20.5–37.5 m depth, submarine cave, totally dark inside; December 1996, 1 specimen.—"Sea Fans Cave" diving site, east of Taungiskika Island, Vava'u Group (18°39.7'S, 174°04.2'W); 7 m depth, submarine cave, gloomy inside; December 1996, 9 specimens.—SOCIETY ISLANDS: Tetuatiare Passage, north of Raiatea (16°49.5'S, 151°29.6'W); 10 m depth; submarine caves, gloomy inside; December 1996, 1 specimen, MNHN.—"Cave Arue" diving site, west of Tahiti Island (17°30.9'S, 149°32.1'W); 22–30 m depth; submarine caves, gloomy inside; December 1996, 12 specimens, MNHN.—"Banc des Daulphins" diving site, west of Tahiti Island (17°29.9'S, 149°38.3'W); 20 m depth; submarine cavern, gloomy inside; December 1996, 103 specimens (50 specimens registered; MNHN).

Distribution and age.—Tropical and subtropical Indo-Pacific (Figure 14). Holocene.

Diagnosis.—Medium-sized *Pisulina* characterized by a thick, globose to obliquely ovate shell, a robust projection on inner lip, and ca. 7 μ m-wide wavy spiral ridges over teleoconch surface; protoconch multispiral, with exposed portion drop-shaped and 155 to 215 μ m in maximum dimension; larval shell with 3 or 4 spiral ridges and many microscopic pits; inner line of inner lip callus continuous with basal lip without a sinus; basal lip with a weak tubercle.

Description.—Shell small, up to 6.7 mm wide and 7.0 mm high, thick, globose to obliquely ovate, with a low spire and a blunt apex (Figure 1). Protoconch multispiral. Embryonic shell covered by larval shell whorls and by first teleoconch whorl to varying degrees based on protoconch inclination, smooth, sometimes with faint wavy ridges near teleoconch suture (Figure 4F); exposed portion of embryonic shell 70 to 90 μ m in maximum dimension. Larval shell coils about 1 volution, surrounded largely by first teleoconch whorl, obliquely ovate, about 360 μ m wide and 250 μ m high,

inclined about 30° to teleoconch (Figure 4A, B, E, F); exposed drop-shaped area 155–215 μ m in maximum dimension, almost smooth except for unevenly spaced growth lines; surface near apertural lip sculptured with 3 or 4 indistinct, ca. 3 μ m-wide, 80 to 140 μ m-long spiral ridges (Figure 4C), and also with many pits more or less irregularly arranged in a spiral direction and sometimes giving rise to short grooves (bearing granules up to 0.5 μ m in diameter) by being connected with one another (Figure 4D). Apertural lip of larval shell biconvex, opisthocline and very discordant with first teleoconch whorl (Figure 4A). Teleoconch coils less than 3.3 in number, smooth to somewhat polished, first whorl coils almost planispirally; teleoconch surface with dense, ca. 7 μ m-wide spiral ridges, subdivided by growth lines (Figure 2A). Aperture narrow and semilunar; outer lip prosocline, angled 35° to 40° to shell axis, beveled and not reflected; inner lip thickened by callus, with a broad, strong, quadrangular projection at its middle and a weak tubercle on the base; inner line of inner lip callus is an inverse-S shape, without sinuation at base. Operculum (Figure 8A) with a paucispiral nucleus 215 to 230 μ m in maximum dimension (Figure 8B); apophysis moderately long and weakly curved spirally.

Remarks.—According to Herbert and Kilburn (1991), the holotype from Southern Province of Sri Lanka (Ceylon) is thought to be in the Indian Museum, Calcutta. We have not examined the type specimen, but there is little possibility of mistaking the shells at hand with any but this remarkable species.

Pisulina adamsiana is a quite distinctive species because it has a single robust quadrangular projection on the inner lip, whereas other modern species have multiple teeth. Moreover, this is the only modern species with a multispiral protoconch (Figure 4) and a paucispiral opercular nucleus (Figure 8B), which strongly suggest a relatively long

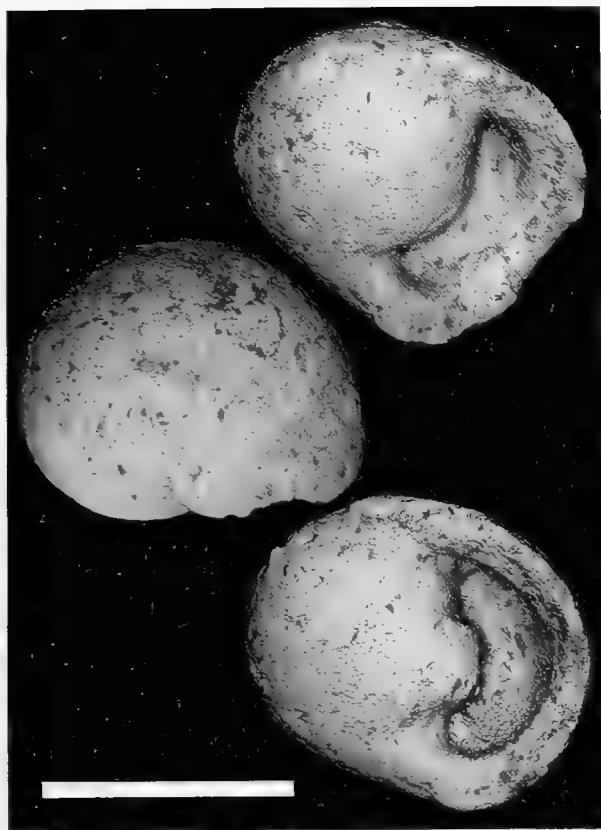


Figure 15. *Pisulina subpacific* Ladd, 1966. Holotype (USNM 648341). Scale bar = 1 mm.

planktotrophic period for this species (see below). Furthermore, *P. adamsiana* differs from other *Pisulina* species by the inner line of its inner lip callus being inversely S-shaped, by the lack of a sinuation between the basal lip and the inner line of the inner lip callus, and by the presence of a weak tubercle on its basal lip (see Table 1).

Intraspecific variation of shell characters is small in this species, perhaps because of genetic homogeneity related to its well-developed dispersion ability. Scheltema (1971) estimated the duration of pelagic stage less than 55 days for *Smaragdia viridis* (Linnaeus, 1758). Taking the smaller size and fewer number of the larval shell whorls into consideration, the planktotrophic period of *P. adamsiana* is assumed to be shorter than that of *S. viridis*.

Koike (1985) described the spermatozoon ultrastructure of "*P. adamsiana* (?)" and stated that the spermatozoon is similar to that in *Clithon retropictus* (Martens, 1879), *Neritina plumbea* Sowerby, 1855, *Neritina variegata* Lesson, 1830, and *Septaria porcellana* (Linnaeus, 1758). However, the sperm of *P. adamsiana* from Sipadan Island is similar to the sperm of *Waldemaria* in Helicinidae rather than to the sperm of neritids (J. Healy, personal communication). It is likely that Koike's (1985) identification of *P. adamsiana* is incorrect.

Pisulina subpacific Ladd, 1966

Figure 15

Pisulina subpacific Ladd, 1966, p. 59, pl. 11, fig. 10.

Material examined.—Holotype from Bikini Island, Bikini Atoll, Marshall Islands; horizon in drill hole, at a depth of 789–799 feet (240–244m), late Miocene, USNM 648341.

Distribution.—Marshall Islands, known only from the type locality. Late Miocene.

Diagnosis.—Small *Pisulina* characterized by a globose and thick shell, a semilunar aperture and a strong quadrangular projection on inner lip; exposed portion of protoconch drop-shaped, ca. 275 μ m in maximum dimension.

Description.—Shell minute, 1.2 mm wide, 1.4 mm high, globose, thick, eroded, creamy in color, opaque, with a very low spire (Figure 15). Protoconch surrounded by first teleoconch whorl, drop-shaped in apical view, and visible portion is ca. 275 μ m in maximum dimension. Teleoconch of 1.5 whorls, with first whorl coiled almost planispirally; exterior surface lacking visible sculpture. Aperture small and semilunar in shape; outer lip prosocline, angled 35° to shell axis; inner lip thick and blunt at margin due to erosion, bearing a large, robust, adaxially convex quadrangular projection ca. 310 μ m wide and ca. 120 μ m high at its midpoint; inner line of inner lip callus inversely S-shaped, strongly concave in parietal area, and continues to basal lip without sinuation.

Remarks.—This Miocene species is known only from the holotype. *Pisulina subpacific* is very similar to *P. adamsiana* in having a large, broad and quadrangular projection on its inner lip. Moreover, the present species seems to possess a multispiral protoconch as seen in *P. adamsiana*, judging from the drop-shaped protoconch that is exposed above the first teleoconch. Ladd (1966) separated this species from *P. adamsiana* based on its smaller shell size and lower spire, but the holotype of *Pisulina subpacific* is unequivocally an immature specimen so these differences cannot be used to separate the two species. Fortunately, there are two characteristics that convincingly separate these two species. In *P. subpacific*, the maximum dimension of the exposed portion of the protoconch is much larger (Table 1), and the inner lip projection is much stronger and twice as large as in *P. adamsiana*.

Pisulina buplicata Thiele, 1925

Figures 2B; 5A, B; 16; 17A

Pisulina buplicata Thiele, 1925, p. 32, pl. 3, fig. 15.

Pisulina adamsiana Nevill and Nevill. Komatsu, 1986, p. 42, 43, pl. 8, fig. 9; Hinoide and Habe, 1991, p. 49 (in part), fig. 2; Fukuda, 1993, p. 31, fig. 120; Sasaki, 1998, p. 117, figs. 78g, h.

Material examined.—Holotype from Indian Ocean ("East India?"), coll. von Finsch, MNHB.—JAPAN: Tsuchihama, Amami-Oshima Island, Kagoshima (28°24.4'N, 129°21.1'E); beach drift; July 1991, 14 specimens.—March 1993, 18 specimens.—Sankakubama, Naze-shi, Amami-Oshima Island (28°23.1'N, 129°30.3'E); beach drift; July 1991, 36 specimens.—Ankyaba, Kakeroma Island, Amami Islands

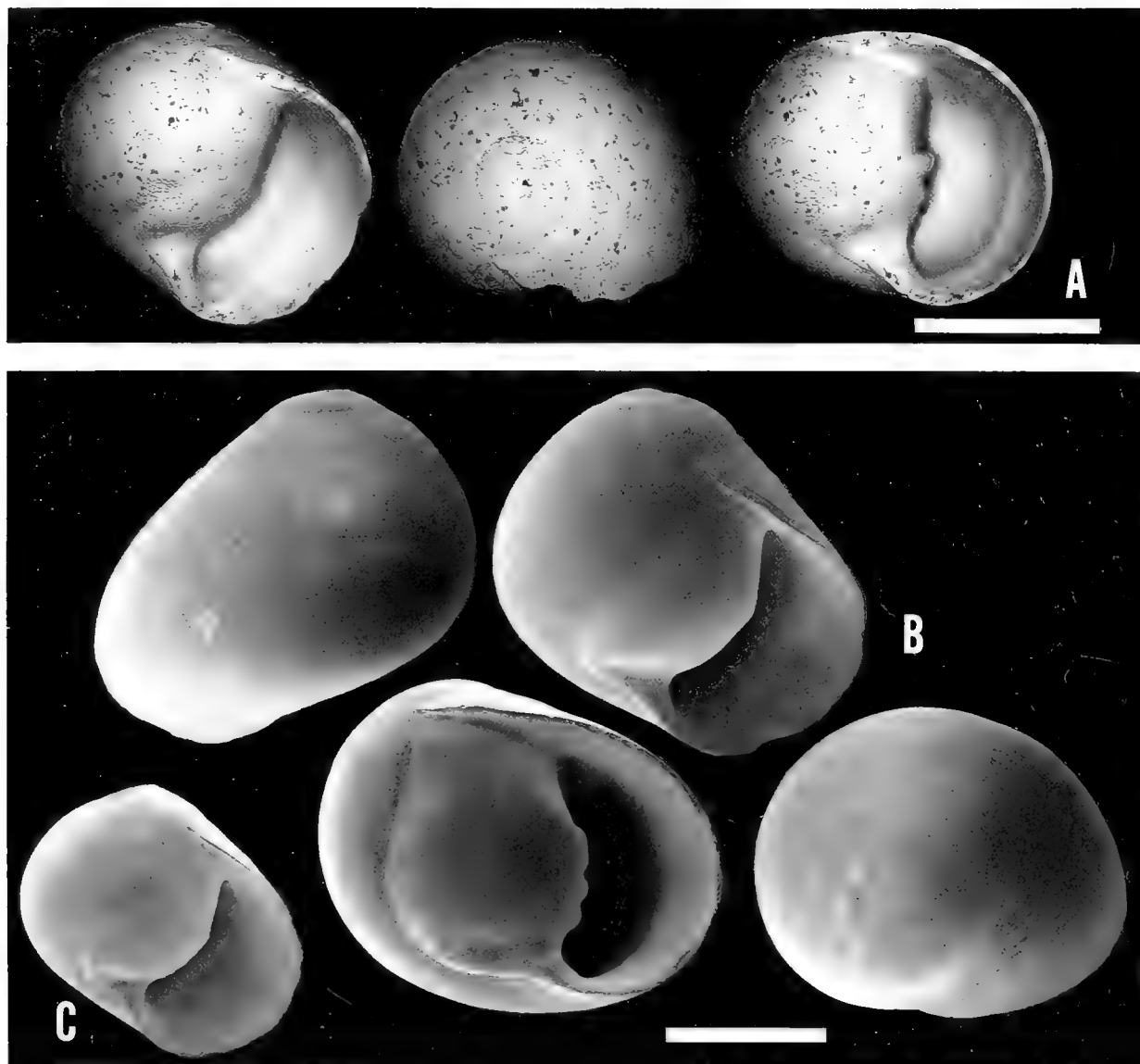


Figure 16. *Pisulina bispicata* Thiele, 1925. **A.** Holotype (MNHB), juvenile shell. Scale bar = 1 mm. **B.** Mature shell (four views) from Shimoji Island, Okinawa (NSMT-Mo71621). **C.** Mature shell (lower left specimen only) from Yap Island (NSMT-Mo71623). Scale bar = 2 mm for B and C.

(28°06.2'N, 129°21.1'E); beach drift; August 1993, 18 specimens. — Kunigami, Okinoerabu Island, Amami Islands (27°25.9'N, 128°42.8'E); beach drift; August 1992, 3 specimens. — "Devil's Palace (= Mao-no-kyuden)" diving site, Shimoji Island, Miyako Islands, Okinawa (24°49.7'N, 125°08.2'E); 25 m depth, submarine tunnels, gloomy inside; 1992, 93 specimens (10 specimens NSMT-Mo71621). — "Cross Hole" diving site, northwest of Irabu Island, Miyako Islands (24°51.6'N, 125°09.5'E); 15 m depth, submarine cave gloomy inside; 4 specimens, coll. M. Taniguchi. — north of Kohama Island, Yaeyama Islands (24°21.5'N, 123°58.9'E); 15–20 m depth, crevices; March 1996, more than 1000

specimens (20 specimens NSMT-Mo71622). — off Nishinohama, Kuroshima Island, Yaeyama Islands (24°14.6'N, 123°59.0'E); 10 m depth, sandy bottom; March 1996, 1 specimen. — PHILIPPINES: Balicasag Island, Panglao, Bohol (9°32.7'N, 123°40.7'E); 14–40 m depth; submarine caverns, gloomy inside; May 1994, 56 specimens. — PALAU: "Siaes Tunnel" diving site, southwest of Siaes dropoff, ca. 6 km west-northwest of Aulong Island, Rock Islands (7°18.7'N, 134°13.6'E); 24–53.5 m depth, huge submarine tunnel; April 1995, 3 specimens. — YAP: "Spanish Wall" diving site, west of Gilman, Yap Island (9°27.2'N, 138°02.5'E); 20–24 m depth, caverns and a small tunnel; November 1997, 18

specimens (6 specimens NSMT-Mo71623).—"Big Bend" diving site, west of Kanifay, Yap Island (9°28.1'N, 138°02.8'E); 8 m depth, a small cave, gloomy inside; November 1997, 4 specimens.—AUSTRALIA: Michaelmas Cay, Great Barrier Reef, Queensland (16°36'S, 145°59'E); May to June 1926, 1 specimen, coll. T. Iredale and G. P. Whitley (G. B. R. Boring Expedition), AMS C-345143.—Green Island, Great Barrier Reef (16°46'S, 145°58'E); May 1926, 1 specimen, coll. T. Iredale (G. B. R. Expedition), AMS C-345144.—East Face, Lizard Island, Great Barrier Reef (14°40'S, 145°29'E); 20 m depth; December 1974, 1 specimen, coll. W. F. Ponder, P. H. Colman and I. Loch, AMS C-345145.—NEW CALEDONIA: east of Nuu Powa islet, Iles des Pins, New Caledonia (22°31.6'S, 169°25.8'E); 17–19.5 m depth, meandering submarine cave, totally gloomy inside; October 1996, 2 specimens, MNHN.—Noumea (22°16'S, 166°27'E); pre-1950, 1 specimen, coll. T. Iredale, AMS C-345147.—VANUATU: White Sands, ca. 40 km from Port Vila, south-east of Efate Island (17°47'S, 168°33'E); March 1975, 2 specimens, coll. P. H. Colman, AMS C-345148.—west of Efate Island (17°39.1'S, 168°11.3'E); cavern; October 1996, 1 specimen.—"Taj Mahal" diving site, west of Efate Island (17°38.4'S, 168°08.7'E); 18 m depth, submarine cave, gloomy to totally dark inside; October 1996, 7 specimens.—FIJI: Nadi Bay (Tomba Ko Nandi), Viti Levu Island (17°44'S, 177°25'E); 9–35 m depth; 1962, 2 specimens, coll. J. Laseron, AMS C-345149.—northwest of Dravuni Island, Great Astrolabe reef (18°42.5'S, 178°29.8'W); 8 m depth, submarine cave, totally dark inside; December 1996, 1 specimen.—northwest of Dravuni Island, Great Astrolabe reef (18°45.3'S, 178°28.0'W); 23–24 m depth, cavern, gloomy to totally dark inside; December 1996, 5 specimens.—north of Ono Island, Great Astrolabe reef (18°51.8'S, 178°27.0'W); depth 7–16 m, submarine tunnel, gloomy inside; December 1996, 13 specimens.—TONGA: east of Fao Island, Ha'apai Group (19°46.5'S, 174°22.6'W); 6–7.5 m depth, submarine tunnel, gloomy inside; December 1996, 2 specimens.—southwest of Mo'ung'one Island, Ha'apai Group (19°38.3'S, 174°29.6'W); 11–28 m depth, cavern; December 1996, 3 specimens.—PITCAIRN GROUP: North Beach, Henderson Island; middle or late Pleistocene sediments in an uplifted cave; 1 specimen, coll. R. C. Preece (Pitcairn Islands Scientific Expedition 1991–2), UMZC.

Distribution and age.—Tropical and subtropical areas of the Indo-Pacific (Figure 14). Middle or late Pleistocene to Recent.

Diagnosis.—Medium-size *Pisulina* characterized by a glossy, thick, globose to pear-shaped shell, a high conical spire, a paucispiral protoconch, a semilunar aperture, and 3 to 5 blunt, somewhat squarish teeth along inner lip; teleoconch surface with microscopic spiral rows of granules.

Description.—Shell small, up to 4.8 mm wide and 5.5 mm high (1.7 mm wide and 1.6 mm high in holotype; Figure 16A), thick, globose to pear-shaped, with a moderately low to rather high conical spire (Figure 16B, C). Protoconch paucispiral, coiling almost planispirally with a slightly angulate periphery, ca. 310 μ m wide and ca. 250 μ m high, not inclined with respect to teleoconch (Figure 5A, B); outer lip of protoconch with faint and fine growth lines, remainder of protoconch smooth except for 15 to 25 indistinct longitudi-

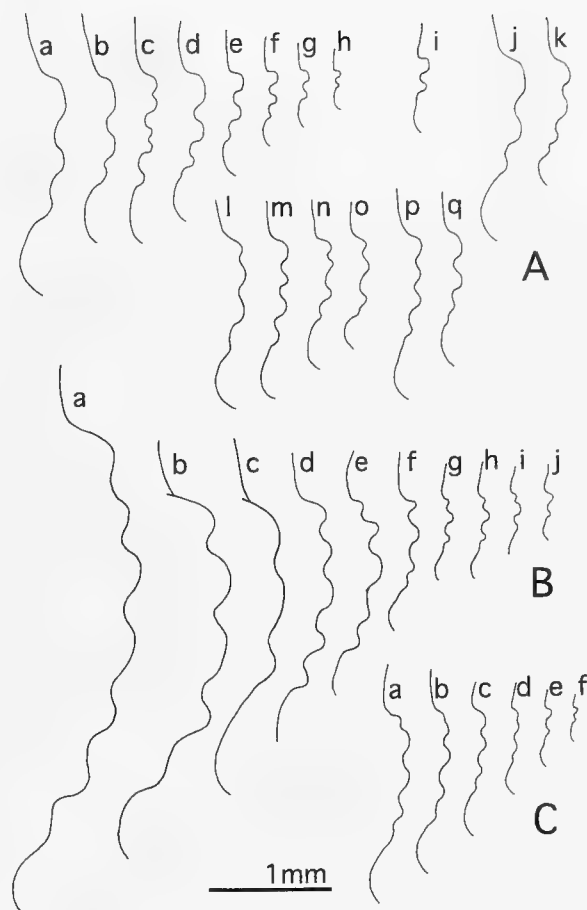


Figure 17. Ontogenetic changes in the apertural teeth of individuals of three *Pisulina* species from different geographic regions, seen in oblique apertural view. **A.** *Pisulina biplicata* Thiele, **a–h**: from Okinawa, **i**: Indian Ocean (Holotype), **j**: the Philippines, **k**: Palau, **l–o**: Yap, **p–q**: Fiji. **B.** *Pisulina maxima* sp. nov., **a**: Saipan Island (Holotype), **b**: the Philippines, **c–j**: Palau. **C.** *Pisulina tenuis* sp. nov., **a–f**: Okinawa.

nal folds; protoconch aperture longitudinally straight and clearly demarcated from teleoconch; visible portion of protoconch 155 to 220 μ m in maximum dimension (ca. 170 μ m in holotype). Teleoconch of up to 3.3 whorls (2.2 in holotype); last whorl inflated and with a small, somewhat concave area below suture; exterior surface smooth and glossy, but weakly sculptured with faint growth lines and microscopic spiral ridges (ca. 1 μ m wide; Figure 2B), consisting of rows of minute granules. Aperture semilunar, small; outer lip prosocline, angled 40° to 50° to shell axis and beveled; inner lip heavily callused with 3 to 5 rather blunt and somewhat squarish teeth at margin (Figure 17A); inner line of inner lip callus convex on columellar area, and continues toward the basal lip with a shallow sinus.

Remarks.—The shell of *P. biplicata* is frequently found as beach drift in southern Japan, but live specimens have not been found. Several opercula most probably from *P. biplicata* have been found together with more than 1000

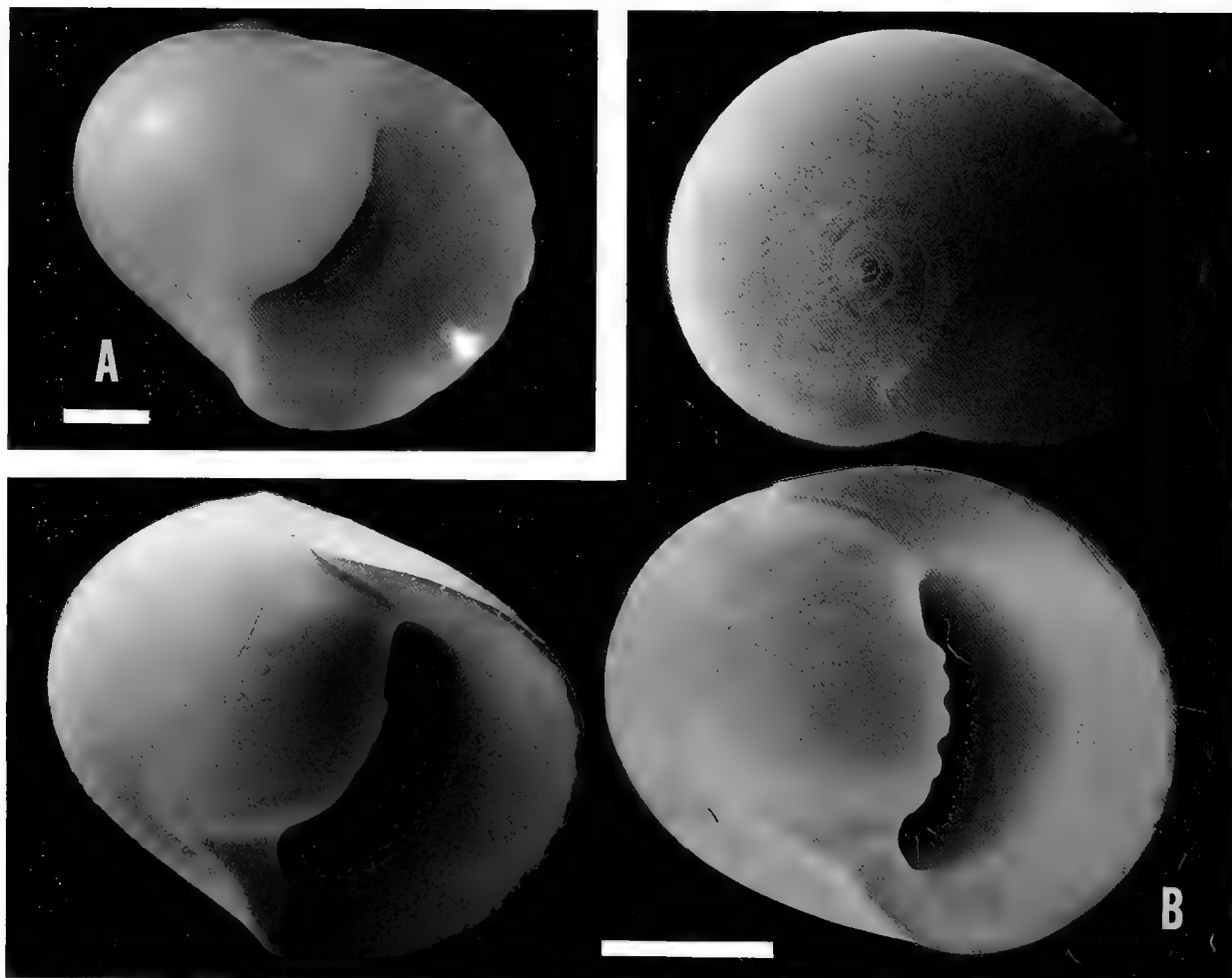


Figure 18. *Pisulina maxima* sp. nov. **A.** Holotype (NSMT-Mo71624) from Saipan. **B.** Paratype (NSMT-Mo71625) from Balicasag Island, Philippine Islands. Scale bars = 2 mm.

empty shells of this species in sediments from crevices north of Kohama Island in Okinawa Prefecture. The operculum of *P. biplicata* is almost identical to that of *P. adamsiana*.

Variation in shell characters is primarily manifested by the number and shape of teeth along the inner lip (Figure 17A). Specimens from Japan and the Philippines generally bear three squarish teeth, while those from Micronesian and southern Pacific islands commonly have more than three round teeth.

Japanese authors have long overlooked *P. biplicata* and misidentified it as *P. adamsiana* (Komatsu, 1986; Hinoide and Habe, 1991; Fukuda, 1993; Sasaki, 1998). Thiele (1925) established *P. biplicata* based on a single specimen and distinguished it from *P. adamsiana* by its supposed lower spire and the presence of two teeth on its inner lip. Unfortunately, these characters cannot be used to separate the two species, because the holotype of *P. biplicata* clearly is an immature specimen. The degree of spire elevation is highly dependent on growth stage, and mature *P. biplicata*

possess the highest spire in this genus. Also, the presence of only two teeth along the inner lip (Figures 16A; 17A-i) is attributed to the immature state of the holotype.

Examination of thousands of specimens from a number of localities clearly reveals that this species can easily be distinguished from *P. adamsiana* by the presence of a paucispiral protoconch, multiple teeth along the inner lip and a sinus in the inner line of the inner lip callus (Table 1). In addition, the shell surface of *P. biplicata* is covered with rows of microscopic granules, while that of *P. adamsiana* is covered with dense microscopic ridges (Figure 2A, B).

***Pisulina maxima* sp. nov.**

Figures 2C; 5C; 9; 17B; 18

Holotype.—NSMT-Mo71624, A huge cave near the "Grotto" diving site, on the northern side of Saipan Island, northern Mariana Islands (15°15.3'N, 145°49.5'N); 20–23.6 m depth.

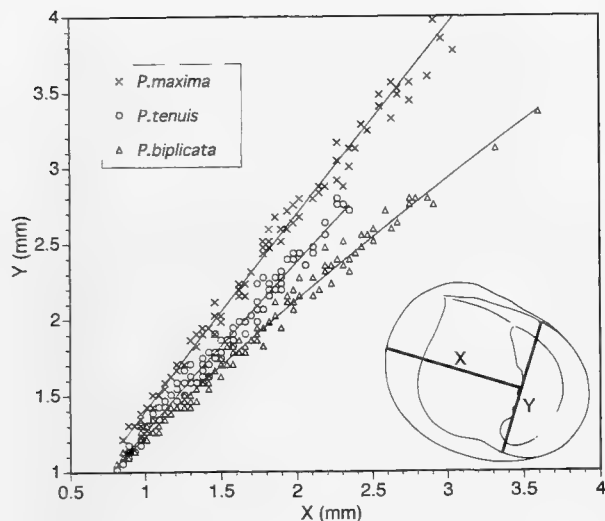


Figure 19. Relationship between the shape of the last whorl and the aperture in three *Pisulina* species: *Pisulina maxima* sp. nov. ($Y=1.668X^{0.945}$, $R^2=0.995$, $n=100$), *Pisulina tenuis* sp. nov. ($Y=1.650X^{0.914}$, $R^2=0.985$, $n=100$) and *Pisulina biplicata* Thiele ($Y=2.417X^{0.789}$, $R^2=0.989$, $n=100$). Specimens were measured in the following way under a microscope with a drawing attachment: X = apertural length from the abapertural margin of whorl to apertural teeth along the axis of the maximum dimension; Y = apertural height along an axis that is perpendicular to X and in contact with the apertural teeth. Shells used for measurements were selected arbitrarily to include all the ontogenetic stages greater than Y = 1 mm. Probabilities that the observed differences in the slopes of the growth lines arose by chance were calculated using a formula shown in Imbrie (1956). This figure shows that *P. biplicata* and *P. tenuis* are significantly different in having distinct slopes ($P < 0.01$); *P. maxima* and *P. tenuis* are meaningfully different ($0.01 < P < 0.05$). Nineteen specimens of *P. maxima* greater than 4 mm in the Y dimension are not plotted in this graph (the largest such specimen attains Y = 7.53 mm).

Paratypes.—JAPAN: Serakaki, Onna, Okinawa Island; 25 m depth, submarine cave; August 1998, 3 specimens, coll. H. Kinjo. —MALAYSIA: "Turtle Cavern", Sipadan Island, west Celebes Sea, Sabah ($5^{\circ}04.8'N$, $118^{\circ}36.5'E$); 9–17 m depth, totally dark inside; May 1997, 17 live individuals. —PHILIPPINES: "Marigondon Cave" diving site, Mactan Island, Cebu ($10^{\circ}15.8'N$, $123^{\circ}59.2'E$); 27 m depth, large submarine cave, totally dark inside; May 1994, 1 specimen. —Balicasag Island, Panglao, Bohol ($9^{\circ}32.7'N$, $123^{\circ}40.7'E$); 14–40 m depth, submarine caverns, gloomy inside; May 1994, 2 specimens (NSMT-Mo71625). —PALAU: "Siaes Tunnel" diving site, southwest of Siaes dropoff, ca. 6 km west-northwest of Aulong Island, Rock Islands ($7^{\circ}18.7'N$, $134^{\circ}13.6'E$); 24–53.5 m depth, huge submarine tunnel; April 1995, 65 specimens; December 1997, 148 specimens (30 specimens NSMT-Mo71626). —"Blue Hole" diving site, northwest of Ngemelis Island, Rock Islands ($7^{\circ}08.3'N$, $134^{\circ}13.3'E$); 36–38 m depth, submarine cave, totally dark inside; December 1997, 2 live individuals. —NORTHERN

MARIANAS: (the type locality); 12–30 m depth, huge cave, gloomy to totally dark inside; November 1997, 24 specimens (10 specimens NSMT-Mo71627); October 1999, 11 specimens. —near "Tinian Grotto" diving site, west of Tinian Island; 50–51 m depth, huge cave, gloomy to totally dark; November 1997, 3 specimens. —AUSTRALIA: "Thundercliff Cave" diving site, Christmas Island ($10^{\circ}28.4'S$, $105^{\circ}36.4'E$); 1.3–6 m depth, totally dark inside; November 1999, 4 specimens.

Distribution and age.—Southeast Asia (Figure 14). Recent.

Diagnosis.—Large *Pisulina* characterized by a subglobose to hemispherical and very thick shell, a paucispiral protoconch with an almost smooth surface, a large semicircular aperture and 3 to 7 teeth along inner lip; microscopic spiral ridges on shell surface are ca. 4 μ m wide.

Description.—Shell medium in size, up to 13.7 mm wide and 12.1 mm high (10.9 mm wide and 9.8 mm high in holotype), very thick, somewhat swollen hemispherical in shape (Figure 18); spire very low and apex pointed. Protoconch paucispiral, a simple low dome-shape in apical view, glossy, smooth, without inclination to teleoconch; visible portion surrounded by teleoconch 180 to 275 μ m in maximum dimension, ornamented by 15 to 25 indistinct longitudinal folds, with faint growth lines on outer lip (Figure 5C); protoconch aperture clearly demarcated from teleoconch by a sharp line. Teleoconch whorls less than 4 in number (3.8 in holotype), striated by microscopic growth lines and spiral ridges ca. 4 μ m wide (Figure 2C), the last whorl coiling nearly planispirally. Aperture semicircular, largely open, prosocline with an angle of 30° to 35° to shell axis; outer lip thick, widely beveled and slightly dilated outward; inner lip covered with a moderately thick callus, convex adaxially at middle, with 3 to 7 dull teeth (Figure 17B); inner line of inner lip callus convex at columellar area and continues to basal lip with shallow concavity. Operculum with a concentric nucleus ca. 220 μ m in maximum dimension (Figure 9C), and bears a long and spirally curved apophysis (Figure 9A, B).

Remarks.—This new species is similar in protoconch morphology to *P. biplicata*, but is primarily distinguished from the latter by its much larger shell size and less glossy teleoconch surface. In addition, the whorls of *P. maxima* expand more rapidly than in *P. biplicata*, so that the former species has a lower spire and a larger aperture than the latter species (Figure 19). This species further differs from *P. biplicata* in the number and shape of the inner lip teeth: *P. maxima* has up to seven rounded teeth, with the largest one located centrally, whereas *P. biplicata* has less than five squarish teeth, with the largest tooth located adapically. In addition, the third tooth ontogenetically appears above the first and second ones in the new species, while it appears below them in *P. biplicata* (Figure 17).

Pisulina tenuis sp. nov.

Figures 2D; 5D, E; 17C; 20

Holotype.—NSMT-Mo71628, "Sabachi Cave," southeast of Yonaguni Island, Yaeyama Islands, Okinawa, Japan ($24^{\circ}26.1'N$, $122^{\circ}57.5'E$); 25–30 m depth, submarine cave,

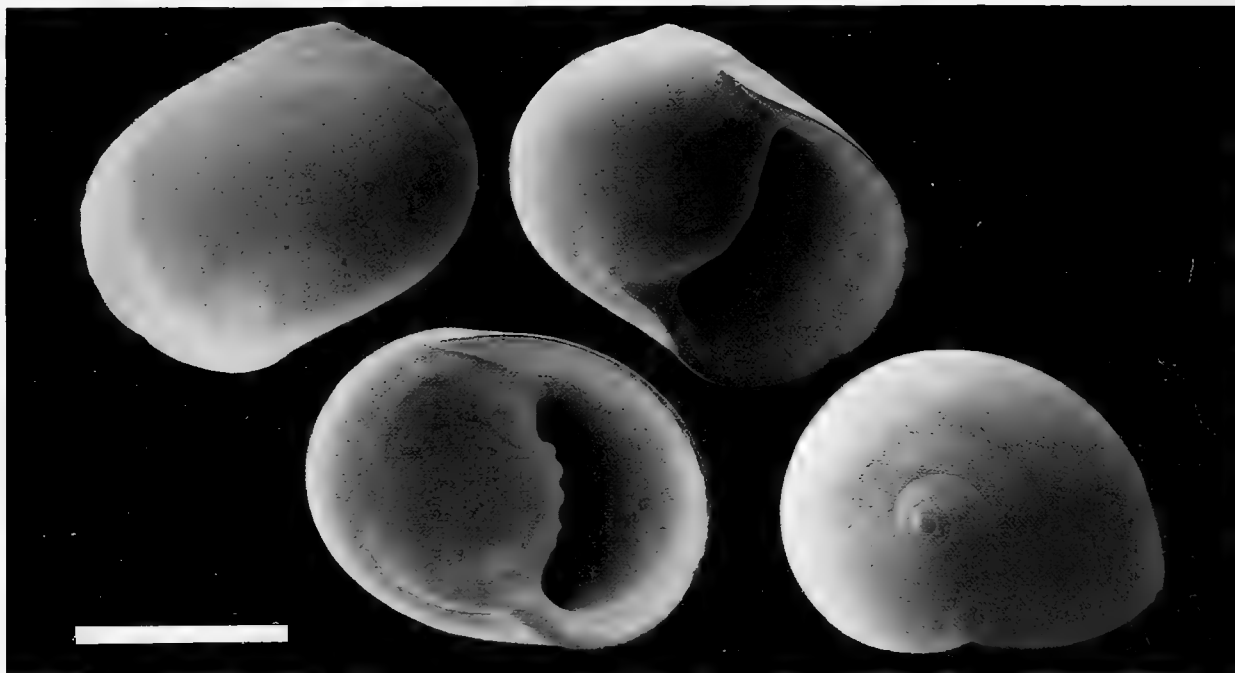


Figure 20. *Pisulina tenuis* sp. nov. Holotype (NSMT-Mo71628) from Yonaguni Island, Okinawa. Scale bar = 2 mm.

totally dark inside.

Paratypes.—More than 1000 specimens from the type locality; September 1994 (100 specimens registered; NSMT-Mo71629).

Distribution and age.—Known only from Yonaguni Island, Japan (Figure 14). Recent.

Diagnosis.—Small *Pisulina* characterized by a thin shell, subglobose to swollen hemispherical shape, a moderately large semicircular aperture, and 4 or 5 teeth along inner lip. Protoconch paucispiral, ovate and smooth. Teleoconch surface with spiral ridges ca. 4 μ m wide.

Description.—Shell small, 4.0 mm wide and 3.6 mm high in largest specimen (3.9 mm wide and 3.5 mm high in holotype), obliquely ovate to hemispherical in shape, and thin but solid. Spire low, with a pointed apex (Figure 20). Protoconch paucispiral, smooth except for 15 to 25 indistinct longitudinal folds near suture, glossy, ca. 330 μ m wide and ca. 270 μ m high, coils almost planispirally, and not inclined to teleoconch (Figure 5D, E); visible portion surrounded by teleoconch 210 to 300 μ m in maximum dimension (ca. 210 μ m in holotype); outer lip sculptured with indistinct growth lines and ridges (Figure 5D); protoconch aperture demarcated clearly from teleoconch and weakly sinuous in its middle part. Teleoconch coils up to 2.9 in number (2.8 in holotype), slightly concave below suture; exterior surface smooth except for faint growth lines and microscopic spiral ridges ca. 4 μ m wide (Figure 2D). Aperture semicircular in shape and widely open; outer lip prosocline, angled 35° to 40° from shell axis, weakly beveled and somewhat thickened on interior; inner lip moderately thick, bearing a convex

adaxial margin and 4 or 5 dull teeth of almost equal strength (Figure 17C); inner line of inner lip callus convex in columellar area and continues to basal lip with a shallow sinus.

Remarks.—*Pisulina tenuis* sp. nov. most closely resembles *P. maxima*, since both species share the same protoconch morphology, shell form and surface microsculpture. The two species are also similar in the number and shape of the inner lip teeth. However, *P. tenuis* clearly differs from *P. maxima* by its thinner shell and smaller shell size (see Table 1). A morphometric analysis shows that *P. tenuis* differs from *P. maxima* in having a smaller Y/X ratio (Figure 19).

Pisulina tenuis has not yet been found alive. Opercula thought to belong to this species were found among a vast number of empty shells at the type locality. The opercular features of *P. tenuis* are the same as seen in *P. adamsiana* and *P. maxima*.

Pisulina sp.

Figure 21

Material examined.—North Beach, Henderson Island, Pitcairn Group; middle or late Pleistocene sediments in an uplifted cave; 2 specimens, coll. R. C. Preece (Pitcairn Islands Scientific Expedition 1991–2), UMZC.

Distribution and age.—Known only from Henderson Island. Middle or late Pleistocene.

Description.—Shell small, thick, up to 4.2 mm wide and 3.8 mm high, hemispherical in outline (Figure 21A). Spire

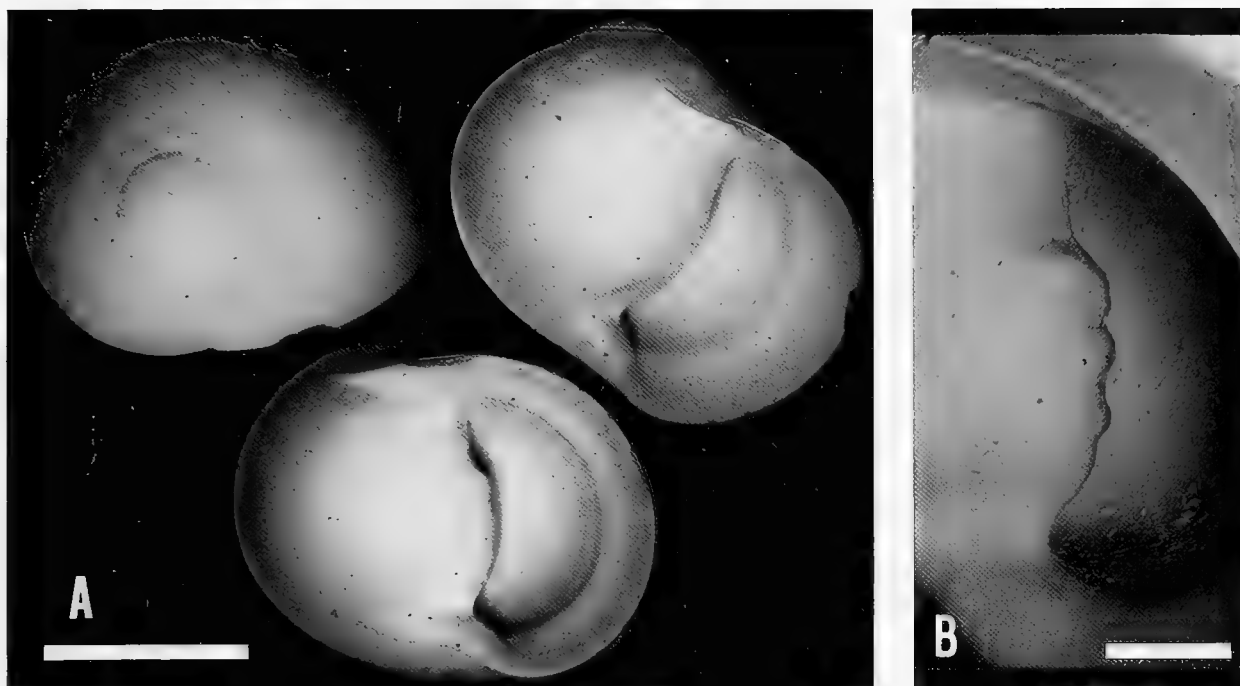


Figure 21. *Pisulina* sp. from Henderson Island, Pitcairn Group (UMZC). **A.** Scale bar = 2 mm. **B.** Oblique apertural view showing details of apertural teeth. Scale bar = 500 μ m.

relatively high, with a protruding apex. Protoconch poorly preserved, smooth, a simple dome-shape, 205 to 240 μ m in maximum dimension and sunken into teleoconch. Teleoconch of up to 3.1 volutions, concave below suture; exterior surface eroded to some extent, but seemingly smooth except for indistinct growth lines. Aperture semicircular and large; outer lip prosocline, angled about 35° to shell axis, beveled and slightly expanded outward; inner lip covered with a moderately thick callus, roundly convex with 4 dull teeth at margin (Figure 21B); inner line of inner lip callus merges into basal lip with a shallow sinus.

Remarks.—This unnamed Pleistocene species is similar to *P. tenuis* in shell size, the shape of its teleoconch whorls, and the number and shape of the teeth on the inner lip (Figure 21B). Moreover, both species have almost the same dimensions for the portion of the protoconch exposed above the teleoconch whorls. This fossil species seems to be distinct from *P. tenuis* by its thicker shell and higher spire, but it is left unnamed until better preserved material is available.

Several fossil specimens similar to this unnamed fossil species have been collected from early to middle Pleistocene sediments on Niue, Cook Islands, by G. Paulay. They differ slightly from *Pisulina* sp. by having a lower spire and fewer teeth on the inner lip, and by the absence of a concavity below the suture of the teleoconch whorls. However, the specimens from Niue cannot be compared in detail, owing to their poor state of preservation.

Acknowledgments

The materials in this paper were collected during the submarine cave expeditions in the tropical Pacific islands for the last 10 years directed by the second author. Special thanks are due to S. Ohashi and S. Kinjo who joined all the expeditions as members and dove many deep caves. Without doubt, our expeditions would have failed had it been without their self-sacrificing cooperation. Other members of the expedition include I. Hayami (Kanagawa University) and G. Paulay (University of Guam), to whom we are acknowledged. We thank the following persons who helped us in various ways: M. Cathrein (Christmas), K. Ekawa (Kagoshima), A. Fielding (Hawaii), R. Gibson (Vanuatu), S. Gori (Italy), B. Holthuis (Guam), H. Kinjo (Okinawa), H. Kubo (Okinawa), C. Meyer (Guam), K. Mochizuki (Palau), K. Ogura (Okinawa), H. Saito (NSMT), M. Severns (Hawaii), J. Starmer (Palau), M. Taniguchi (Okinawa) and Y. Yamazaki (Palau). ORSTOM (Noumea) and the University of the South Pacific gave facilities and logistic support for our expeditions in New Caledonia and Fiji, respectively. We also thank the following for the loan of materials: M. Glaubrecht (MNHB), I. Loch (AMS) and J. Thompson (USNM). This study was supported by grants to T. K. from the Ministry of Education, Science and Culture, Japan (nos. 06454003, 08041162, 11691196 and 11833018), the Fujiwara Natural History Foundation, and the Research Institute of Marine Invertebrates.

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A new potamolepid freshwater sponge (Demospongiae) from the Miocene Nakamura Formation, central Japan

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Abstract. The freshwater sponge *Oncosclera kaniensis* sp. nov. of the demospongian family Potamolepidae is described from the Early Miocene Nakamura Formation (Mizunami Group) in Gifu Prefecture, central Japan. This is the first fossil record of the Potamolepidae in the world and also is the first documentation of fossil sponges from the Nakamura Formation. Paleoecology of *Oncosclera kaniensis* sp. nov. is briefly discussed.

Key words: freshwater sponge, Potamolepidae, *Oncosclera*, Early Miocene, Nakamura Formation

Introduction

A number of well preserved sponges assignable to a new species of the genus *Oncosclera* Volkmer-Ribeiro, 1970 of the family Potamolepidae (Demospongiae) were recovered from the Early Miocene Nakamura Formation, Mizunami Group in Gifu Prefecture, central Japan. This is the first fossil record of the genus *Oncosclera* as well as of the family Potamolepidae. The discovery dramatically extends the fossil record of the family Potamolepidae back to the Early Miocene. Recent species of potamolepid sponges are distributed in South America, Africa, and Asia, and have been considered as Gondwanian elements (Volkmer-Ribeiro and De Rosa-Barbosa, 1978). The discovery of a fossil potamolepid sponge from Japan is very important for future paleogeography and phylogenetic analysis. The purpose of this paper is to describe a new species and discuss its paleoecology.

Geologic setting

The fossil sponges were collected from tuffaceous sandstone exposed on a riverbed of the Kiso River, Dota area of the Minokamo basin, Kani City, Gifu Prefecture, central Japan (Figure 1). Distributed in this riverbed is the Mizunami Group, a stratotype of the Lower to Middle Miocene in Japan, that is composed of nonmarine sediments, while the group is composed of marine sediments in the neighboring Mizunami and Iwamura basins.

A recent detailed lithostratigraphical study of the Mizunami Group along the Kiso River in the Minokamo basin by Shikano (1995) has shown that the group can be divided into three formations in ascending orders: the Hachiya Formation, Nakamura Formation, and Hiramaki Formation.

The Nakamura Formation, from which the fossil sponges were recovered, is 130 m thick, of fluvial and lacustrine origin, and subdivided into the Lower Member, Middle Member, and Upper Member. The potamolepid sponges described here were recovered from a sandstone layer of the Upper Member, about 2 m below the contact with the Hiramaki Formation (Figure 2). The Upper Member is estimated to be 30 m thick and consists of tuffaceous mudstone, sandstone, conglomerate, and lignite. The basal layer of the Upper Member consists of massive tuff, and was dated as 21.7 ± 1.5 Ma by the fission track method (Shikano, 1995).

The sponge-bearing sandstone layer is ill-sorted and contains much granular material and organic debris. Other fossils associated in this sandstone layer are diatoms, macroplants, molluscs, fishes, and mammals. The fossil molluscs in this sandstone include an undescribed viviparid gastropod, *Bellamya* sp. and undetermined unionid bivalves such as *Anodonta* sp. and "*Unio*" sp. The fossil fishes were identified as *Cypris* sp., Cyprininae gen. et sp. indet., and Cultrinae gen. et sp. indet. (Yasuno, 1982; 1983). The fossil molluscs and cyprinids are all permanent freshwater dwellers. The fossil mammals from the sandstone layer are *Plesiosorex* sp., *Amphilagus* sp., *Youngofiber sinensis*, *Anchitheriomys* sp., *Pseudotheridomys* sp., and *Apeomys* (?) sp. (Tomida and Setoguchi, 1994; Tomida and Goda, 1995; Tomida *et al.*, 1995).

Systematic description

Class Demospongiae Sollas, 1885
Order Hadromerida Topsent, 1894
Family Potamolepidae Brien, 1967
Genus *Oncosclera* Volkmer-Ribeiro, 1970

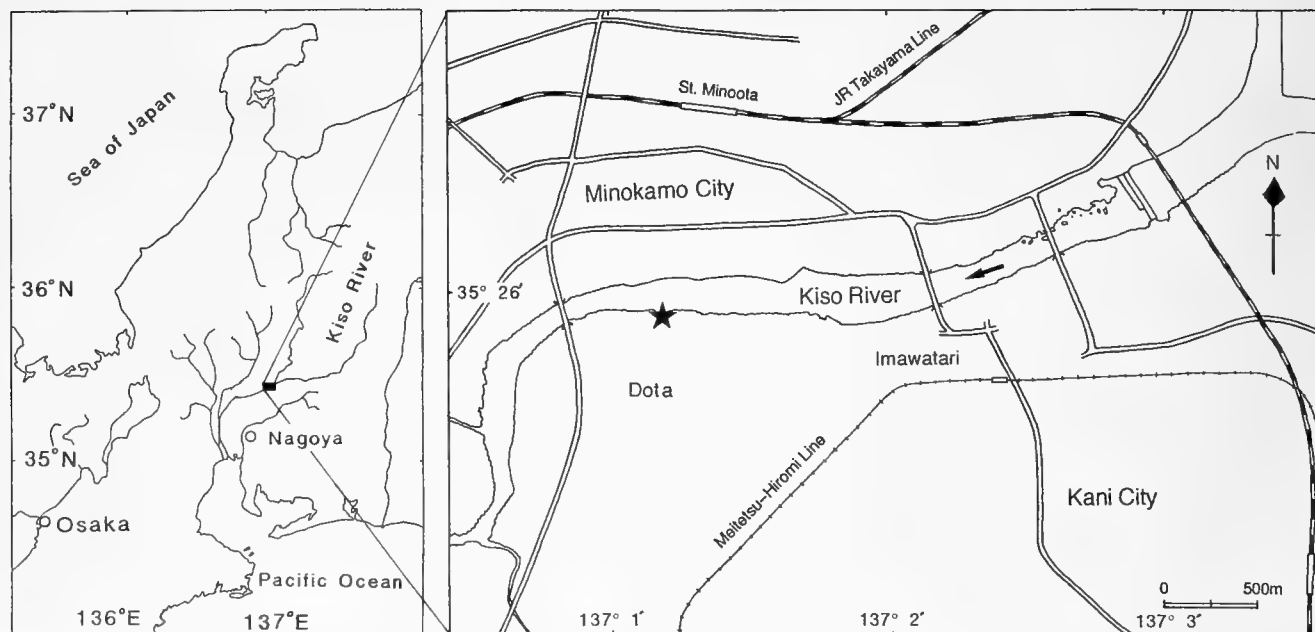


Figure 1. Map showing the sponge locality of the Nakamura Formation, Dota, Kani City.

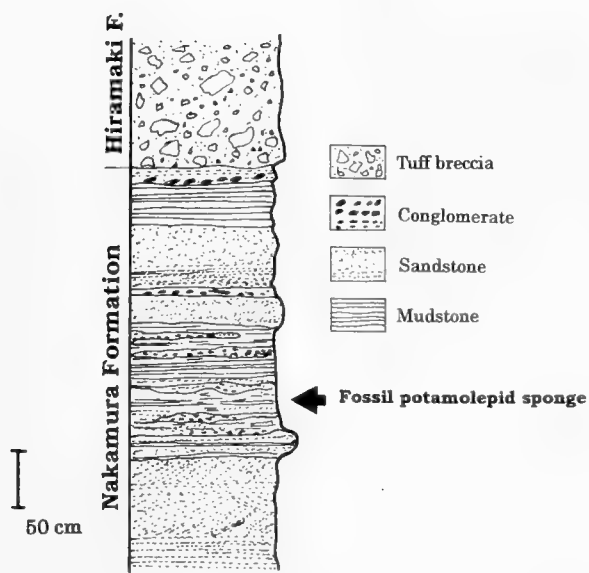


Figure 2. Columnar section showing the sponge-bearing horizon in the Nakamura Formation.

Type species: *Spongilla jewelli* Volkmer, by original designation.

Diagnosis.—Megascleres slightly curved, stout, occasionally microspined, amphioxea to amphistrongyla. Microscleres absent. Gemmoscleres short, stout, feebly curved, extremely variable, amphistrongyla or amphioxea, swollen at central portion, usually spined; spines more numerous at both ends.

Discussion.—Brien (1967) proposed the new family Potamolepididae for the Ethiopian genera *Potamolepis* and *Potamophloios*. The family consists of six genera: *Oncosclera*, *Uruguaya*, *Sterrastrolepis*, *Potamolepis*, *Potamophloios*, and *Stratospongilla*, and the family is considered to have been derived from a certain marine group of the order Hadromerida (Volkmer-Ribeiro and De Rosa-Barbosa, 1978). Of the six genera above, *Oncosclera*, *Uruguaya* and *Sterrastrolepis* from South America have been thought in part to be relicts of the Gondwanian fauna (Volkmer-Ribeiro, 1981).

Oncosclera was originally introduced as a genus of the family Spongillidae by Volkmer-Ribeiro (1970), which included two living species in Brazil, *O. jewelli* (Volkmer, 1963) and *O. navicella* (Carter, 1881). This genus is very close to the genus *Stratospongilla*, but differs from the latter in the absence of microscleres. The genus *Oncosclera* from South America consists of ten species: *Oncosclera petricola* (Bonetto and Ezcurra, 1967), *O. stolonifera* (Bonetto and Ezcurra, 1967), *O. schubarti* (Bonetto and Ezcurra, 1967), *O. ponsi* (Bonetto and Ezcurra, 1968), *O. tonollii* (Bonetto and Ezcurra, 1968), *O. atrata* (Bonetto and Ezcurra, 1970), *O. spinifera* (Bonetto and Ezcurra, 1973), and *O. intermedia* (Bonetto and Ezcurra, 1973) by Volkmer-Ribeiro (1981), who suggested that the number will be reduced by synonymies in future studies. *Spongilla* (*Stratospongilla*) *diahoti* Rützler, 1968 from northern New Caledonia was transferred to the genus *Oncosclera* by Volkmer-Ribeiro and Rützler (1997). According to Volkmer-Ribeiro (1970, 1981), *Spongilla rousseletti* Kirkpatrick, 1906 and *S. (Stratospongilla) shulbotzi* Weltner, 1913 from central Africa, *S. (Stratospongilla) gilsoni* Topsent, 1912 from the Fiji Islands, and *S. clementis* Annandale, 1909 from the Philippines belong to the genus *Oncosclera*.

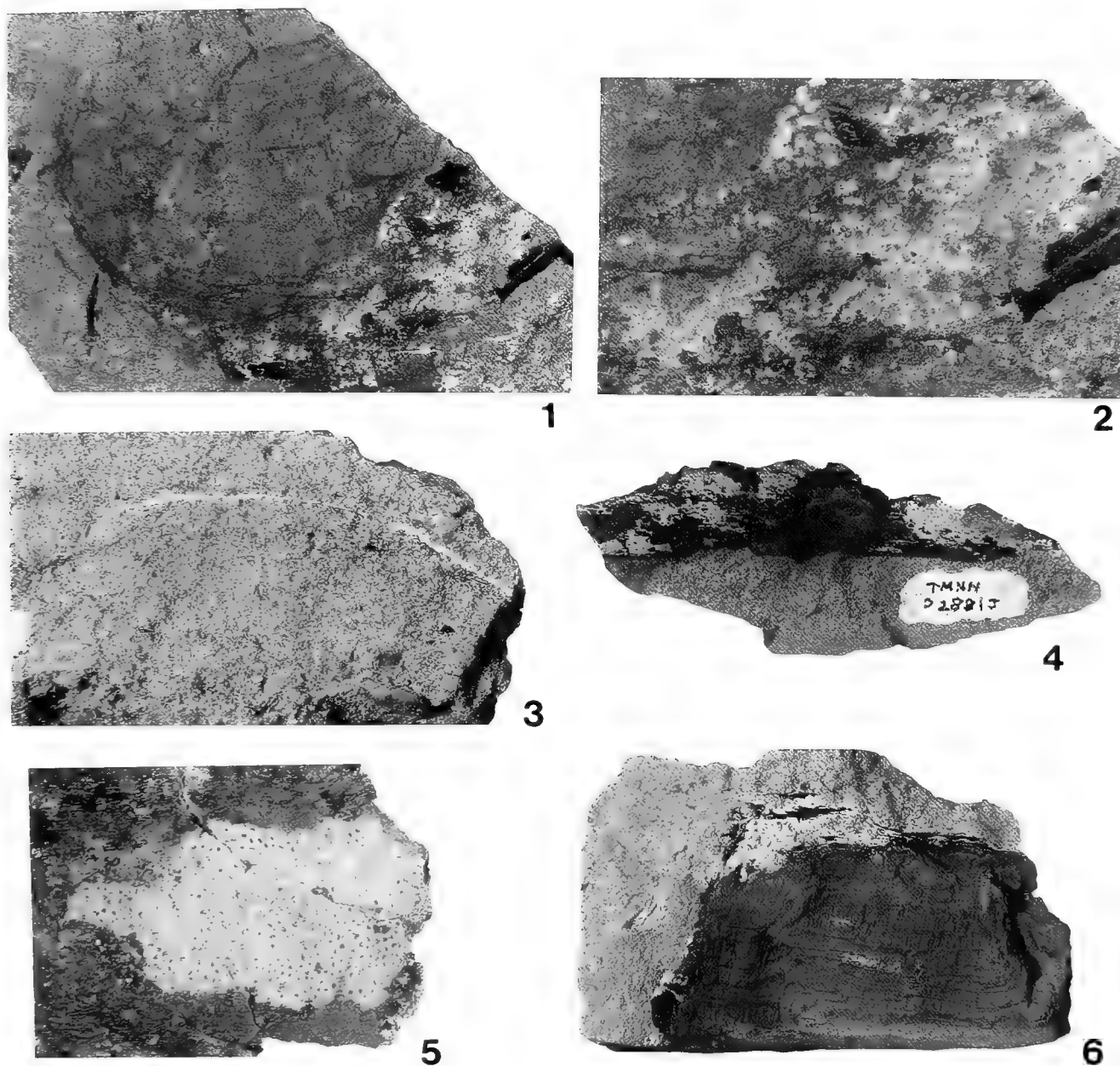


Figure 3. *Oncosclera kaniensis* sp. nov. 1. Sponge bodies encrust the postero-ventral area of the left valve of *Anodonta* sp., TMNH-02882 (paratype), $\times 1$. 2. Enlargement of the sponge bodies of TMNH-02882, $\times 2.1$. 3. Sponge bodies encrust the surface of *Anodonta* sp., vertical section, TMNH-02889a (paratype), $\times 1.2$. 4. Sponge bodies encrust the surface of a cortex fragment (black color), TMNH-02881j (holotype), $\times 1.2$. 5. Attached surface of sponge bodies, TMNH-02886 (paratype), showing the outline of the gemmules represented by ring spots, $\times 2.0$. 6. Sponge bodies encrust the surface of a wood fragment, TMNH-02887, $\times 1.2$.

***Oncosclera kaniensis* sp. nov.**

Figures 3–5

Type locality.—Riverbed on the Kiso River, Dota, Kani City, Gifu Prefecture, Japan (Figure 1).

Etymology.—The species name is after Kani City, the mu-

nicipality of the type locality.

Material studied.—Twenty-two specimens. Holotype: TMNH-02881 a–m, on 13 isolated blocks. Paratypes: TMNH-02885, 2883a, b, 02882, 02884 a, b, 02886. All deposited in the Toyohashi Museum of Natural History.

Diagnosis.—A species of *Oncosclera* characterized by

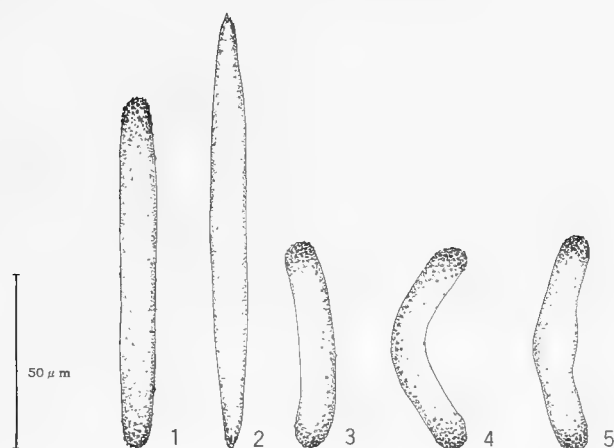


Figure 4. Spicular components of *Oncosclera kaniensis* sp. nov. 1. Amphistrongylous megasclere. 2. Amphioxeous megasclere. 3–5. Three forms of gemmoscleres. Scale bar = 50 μ m.

domination of amphistrongylous megascleres, small amount of amphioxeous megascleres, amphistrongylous gemmoscleres, and dense covering of spines at both ends.

Description.—Sponge encrusting shell surfaces of bivalve and wood fragments. Sponge surface even and generally less than 1 mm in thickness. Skeletal components consisting of megascleres and gemmoscleres. Gemmules with round spots, firmly adhering to basal part of sponge body, about 500 μ m in diameter, but compressed subspherically. Megascleres moderately small, almost straight, solid, amphistrongyla to amphioxea, covered with distinct spines at both ends, 100 to 179 μ m in length and 7 to 15 μ m in thickness. Majority of megascleres stout and cylindrical amphistrongyla (Figure 4.1), occasionally with a few intermixed true amphioxea (Figure 4.2). Microscleres absent. Gemmoscleres stout, variably curved, inflated at middle (Figure 4.3–4.5); amphistrongyla densely covered with distinct spines that are numerous at both ends; some of spines polyfurcate, and inner curved area smooth, 23 to 100 μ m in length, 4 to 7 μ m in thickness.

Comparison.—The present new species is assigned to the genus *Oncosclera* in its shape and surface ornamentation of megasclere and gemmosclere. The new species is similar to the following Recent species from Argentina: *Oncosclera ponsi* (Bonetto and Ezcurra, 1968), *Oncosclera atrata* (Bonetto and Ezcurra, 1970), and *Oncosclera tonollii* (Bonetto and Ezcurra, 1968). Of the three species *O. kaniensis* sp. nov. is most similar to *Oncosclera ponsi* in spicular components, but it differs in having spinose amphioxeous megascleres. The present new species differs from *Oncosclera atrata* from the Parana River, Argentina in having amphistrongyla densely covered with distinct spines at both ends of the gemmoscleres. It also differs from *Oncosclera tonollii* from the Uruguay River, Argentina (Bonetto and Ezcurra, 1967) in having a less spinose surface of gemmoscleres and megascleres. This new species has gemmoscleres similar to the Recent species *Oncosclera*

jewelli (Volkmer, 1963) known only from the Tainhas River of Brazil (Volkmer-Ribeiro, 1970) and *O. schubarti* (Bonetto and Ezcurra, 1967) from the Uruguay River, Argentina, but differs distinctly from the latter species in its spinose amphistrongylous and amphioxeous megascleres.

Paleoecology.—Potamolepids commonly have highly silicified skeletons and lack spongin fibers. Many species of the genus *Oncosclera* encrust stable bottom surfaces in streams. *Oncosclera atrata* inhabits a curved bank of a tributary of the Parana River in the Misiones Province, Argentina, where it encrusts surfaces of partly submerged rocks (Bonetto and Ezcurra, 1970). *Oncosclera ponsi* and *O. tonollii* encrust rocky bottoms in rapid and turbulent waters in the Uruguay River (Bonetto and Ezcurra, 1968). Both species grow in the upper and lower surfaces of the rocks, and the sponges encrusting the lower surfaces are disposed to grow exuberantly. *Oncosclera jewelli* in the Tainhas River of Brazil also encrusts exclusively stable bottom surfaces in fast streams close to rapids and/or falls. *Oncosclera navicella* in the Amazon River of Brazil and Iguazu Fall of Argentina, on the other hand, encrusts ligaments and valves of the living freshwater bivalve *Anodontites trapesialis forbesianus* and *Paxyodon syrmatophorus* (Volkmer-Ribeiro, 1970; Tavares and Volkmer-Ribeiro, 1997).

Oncosclera kaniensis sp. nov. is represented entirely by fossilized sponge bodies and encrusts two types of substrates: shell surface of the unionid bivalve *Anodonta* sp. (Figure 3.1–3.3) and surface of wood fragments (Figure 3.4–3.6). The sponge bodies on the unionid bivalve encrust the ventral and posterior parts of almost horizontally embedded articulated valves that are preserved as composite moulds (Figure 6.1). They also encrust the outer surfaces of isolated valves that are diagenetically compacted and embedded with the convex side up (Figure 6.2). The sponge bodies also encrust strongly compacted woods almost entirely (Figure 6.3) and encrust partly the wood fragments that remain in possession of annual rings (Figure 6.4). The shells and wood fragments may have provided hard substrates for colonization of the fossil sponges in the soft bottom environment. The gemmules of *O. kaniensis* sp. nov. can be seen by naked eye as ring spots. The gemmules of the fossils are located at the basal portion of the sponge as in *O. jewelli* and *O. navicella* (Figure 3.5). These facts strongly suggest that *O. kaniensis* sp. nov. dwelled in a river like the Recent *Oncosclera* species and had a habitat preference to the upper and lower surfaces of hard substrates (Figure 6.5–6.8). The unusual preservation of the megascleres and gemmoscleres of *O. kaniensis* sp. nov. may have resulted from its comparatively stout skeleton, strong attachment to the substrates and rapid burial after death.

Acknowledgments

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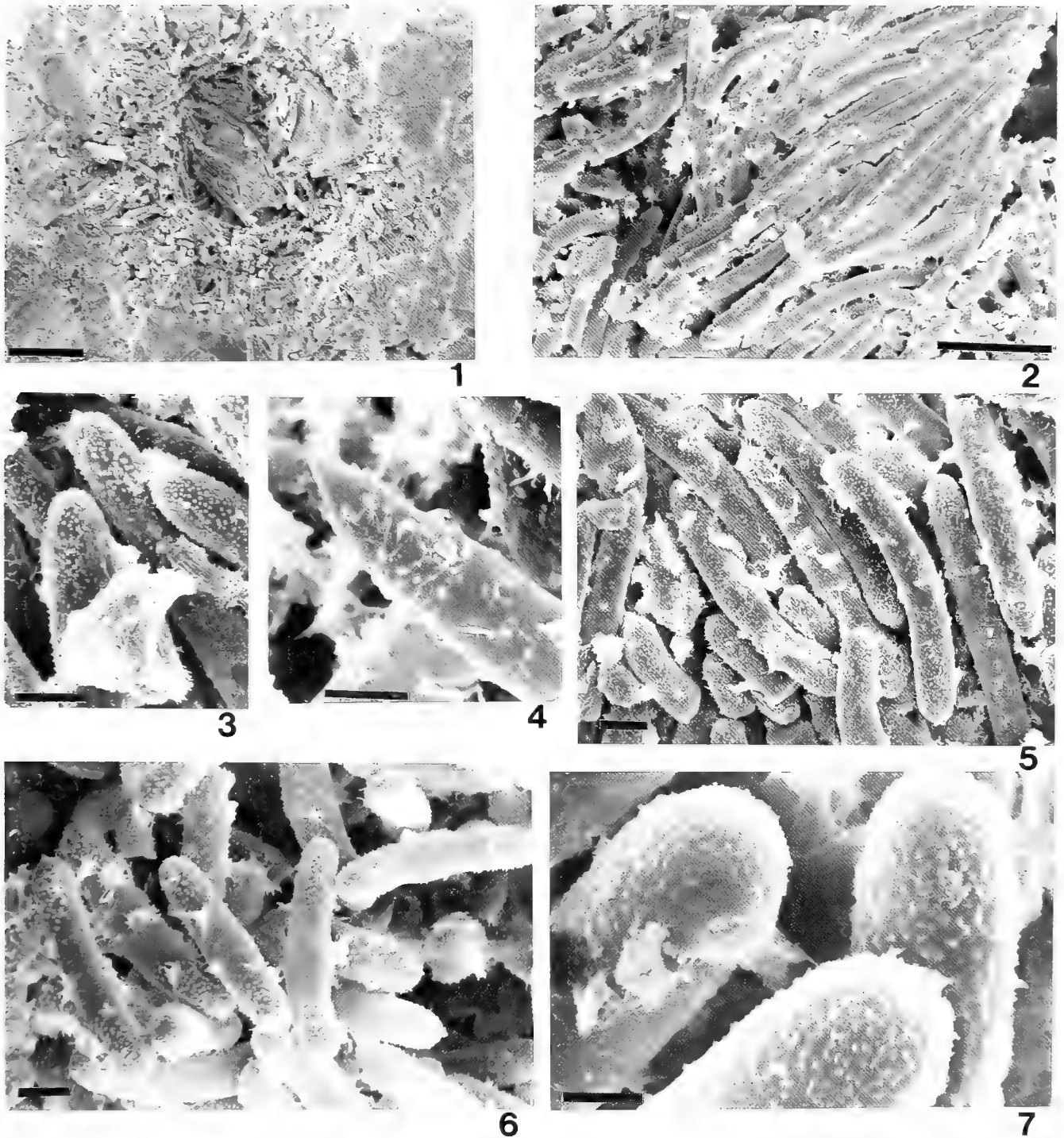


Figure 5. SEM micrographs of *Oncosclera kaniensis* sp. nov. 1. Gemmule, vertical section, scale bar=100 μ m. 2. Amphistrongylous megascleres, scale bar=50 μ m. 3. End parts of amphistrongylous megascleres, scale bar=10 μ m. 4. End parts of amphioxeous megascleres, scale bar=5 μ m. 5. Gemmoscleres, scale bar=10 μ m. 6. Gemmoscleres, scale bar=10 μ m. 7. End parts of gemmoscleres, scale bar=5 μ m.

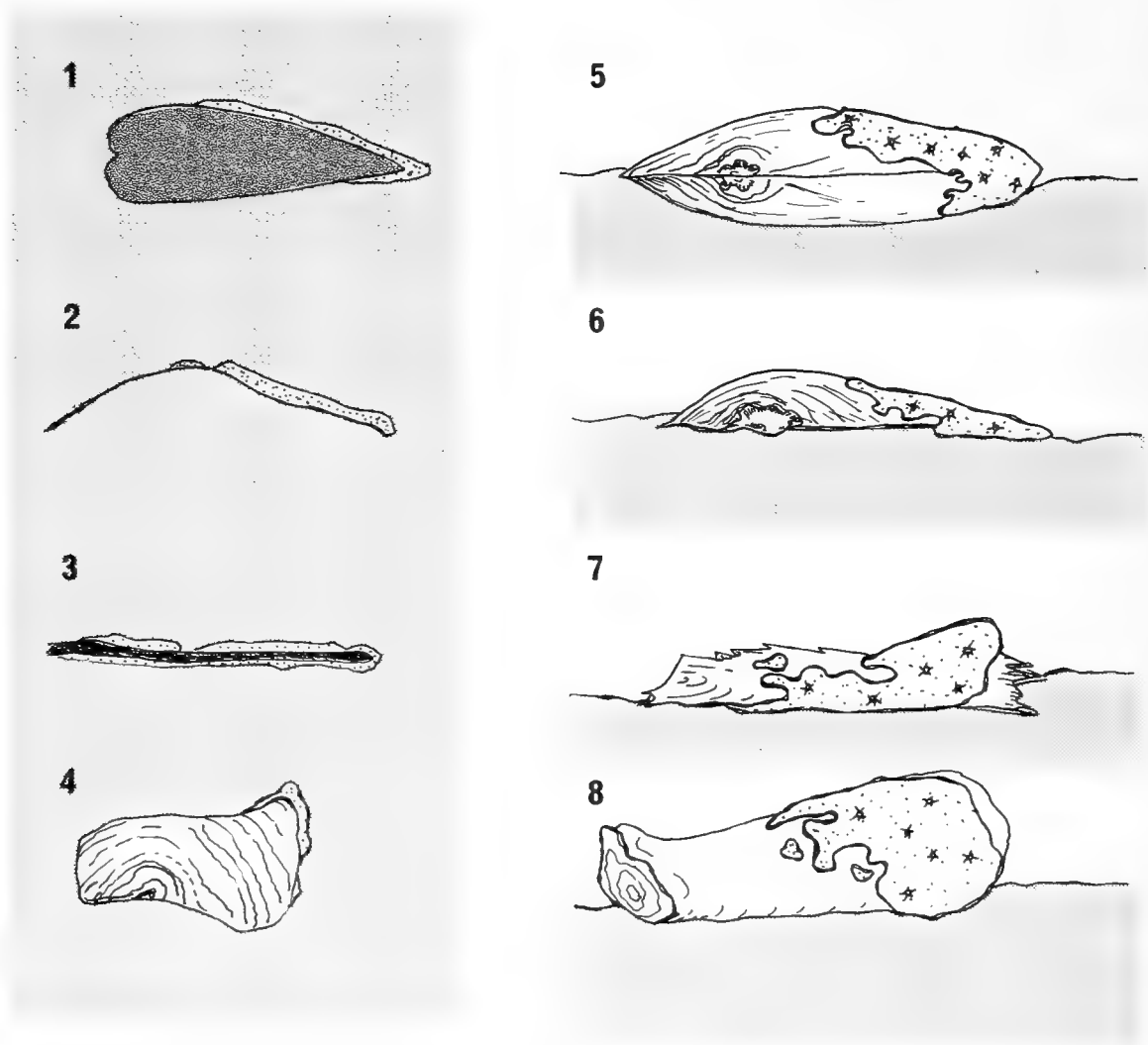


Figure 6. Mode of occurrences of *Oncosclera kaniensis* sp. nov. 1-4. Four types of encrustation. 1. Sponge bodies encrust an articulated valve of the unionid bivalve *Anodonta* sp. The bivalve is embedded with its commissure plane almost horizontal and is preserved as a composite mould. 2. Sponge bodies encrust the outer surface of an isolated valve of the unionid bivalve *Anodonta* sp. The valve is compacted diagenetically. 3. Sponge bodies encrust a strongly compacted wood fragment almost entirely. 4. Sponge bodies encrust a wood fragment that retains its annual rings. 5-8. Reconstruction of the four types of encrustation for 1 to 4, respectively.

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Additions to Cretaceous decapod crustaceans from Hokkaido, Japan—Part 1. Nephropidae, Micheleidae and Galatheidae

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Abstract. Four new species of decapod crustaceans are described from the Upper Cretaceous Upper Yezo Group in Hokkaido, Japan. The monotypic genus *Paki* (Thalassinidea, Micheleidae) is erected with *P. rurkonsimpu* sp. nov. *Hoploparia kamuy* sp. nov. (Astacidea, Nephropidae) represents the first record of the genus *Hoploparia* from the Turonian-Santonian of Japan. *Luisogalathea* gen. nov. (Anomala, Galatheidae), erected with the type species *L. tomitai* sp. nov., contains two North American Cretaceous species, *Galathea cretacea* Stenzel and *Eomunidopsis cobbani* Bishop. *Eomunidopsis kojimai* sp. nov. (Anomala, Galatheidae) represents the first record of the genus from the North Pacific realm.

Key words: Crustacea, Decapoda, Hokkaido, Japan, Upper Cretaceous, Upper Yezo Group

Introduction

The Upper Cretaceous decapod Crustacea from Hokkaido comprises nine species, *Linuparus japonicus* Nagao, 1931 (Palinura, Palinuridae), *Callianassa ezoensis* Nagao, 1941 (Thalassinidea, Callianassidae), and seven brachyurans (Collins, Kanie and Karasawa, 1993). In the present paper we describe four additional new species, one astacidean, one thalassinidean and two anomalans, from the Upper Yezo Group of Hokkaido.

The described specimens are deposited in the Mikasa City Museum (MCM) and the Mizunami Fossil Museum (MFM).

Systematic paleontology

Infraorder Astacidea Latreille, 1802
Superfamily Nephropoidea Dana, 1852
Family Nephropidae Dana, 1852
Subfamily Homarinae Huxley, 1879
Genus *Hoploparia* McCoy, 1849

Type species.—*Astacus longimanus* Sowerby, 1826 by subsequent designation by Rathbun, 1926.

Hoploparia kamuy sp. nov.

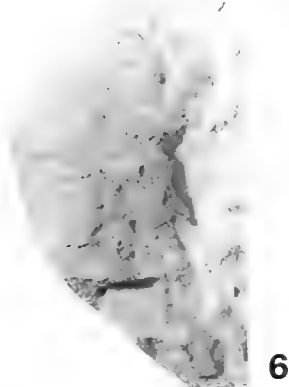
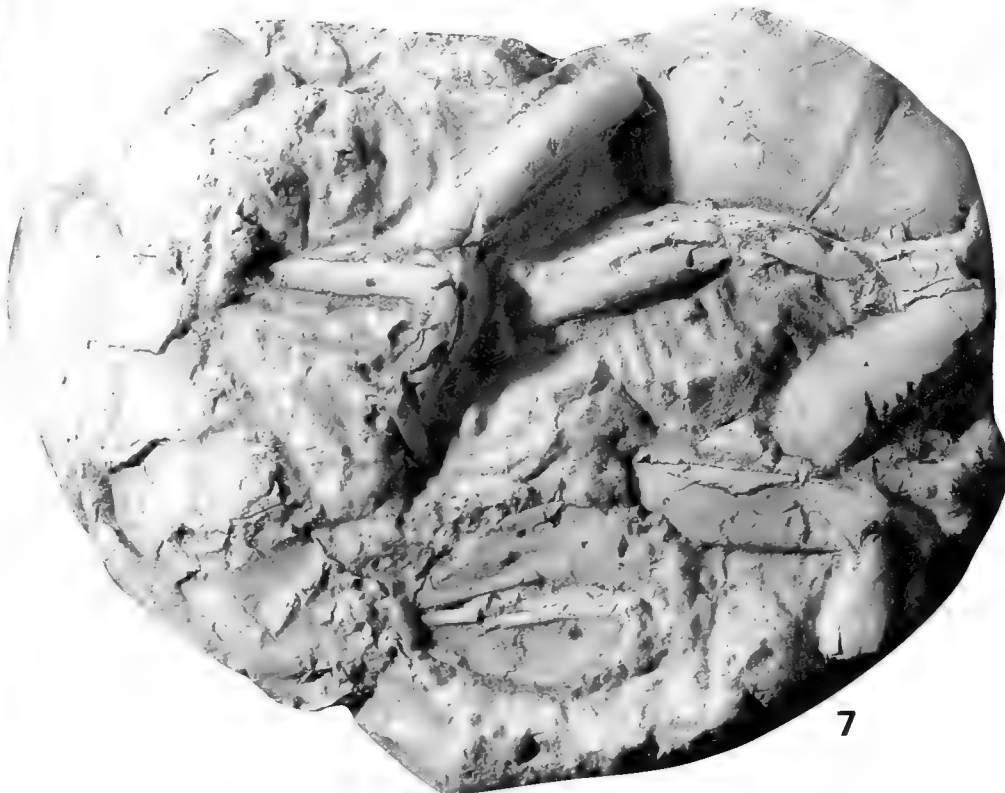
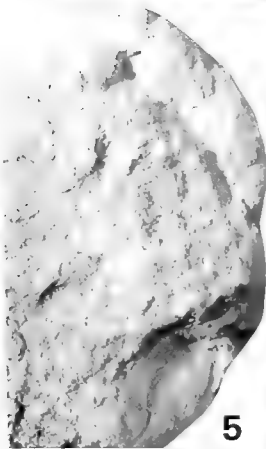
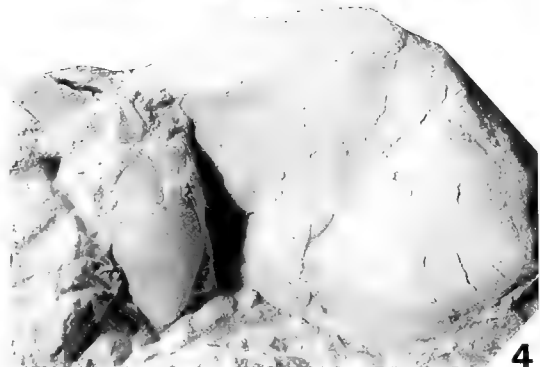
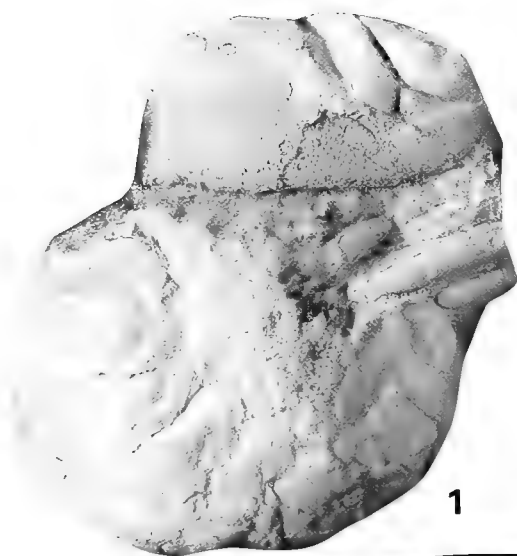
Figure 1.1, 1.2, 1.5, 1.6

Diagnosis.—Moderate-sized *Hoploparia*. Carapace with well developed grooves on anterior half. Antennal region bearing antennal ridge and one postantennal spine.

Abdominal somites simple without tubercles and spines.

Description.—*Hoploparia* with moderate-sized body. Carapace laterally compressed. Rostrum and posterior part of carapace lacking. Surface finely granulated. Orbit small, rounded, bordered by narrow, rounded ridge. Postcervical groove well defined, deep, broad, obliquely extending ventrally, becoming shallower at junction with hepatic groove. Branchiocardiac groove weak. Intercervical groove shallow, extending anteroventrally to, but not joining cervical groove. Second intercervical groove broad, shallow, extending to cervical groove. Hepatic groove shallow, curving to join antennal and cervical grooves. Cervical groove well defined, deep, slightly arcuate, parallel to postcervical groove, extending ventrally to join antennal groove. Antennal groove weakly arcuate, well defined over prominence omega. Prominence omega well defined, triangular. Gastro-orbital groove shallow, extending to near upper part of cervical groove. Antennal region with antennal ridge and with small, forwardly directed postantennal spine. Metorbital spine present, small. Supraorbital and postorbital spines wanting.

Terga of abdominal somites 1–5 smooth, but tergum of somite 6 finely pitted; tergum of somite 1 short; somite 2 largest of all terga. All pleura of somites finely punctuate. Pleuron of somite 1 reduced. Pleuron of somite 2 subrectangular; margins gently convex; anteroventral and posteroventral corners smoothly rounded; surface with marginal furrows joining transverse furrow on anterior part of tergum. Pleura of somites 3–5 triangular, transversely convex with sharp, posteroventral corners with shallow, broad marginal furrow along posterior margin. Pleuron of somite 6 reduced. Telson broken, but dorsal surface finely pitted.



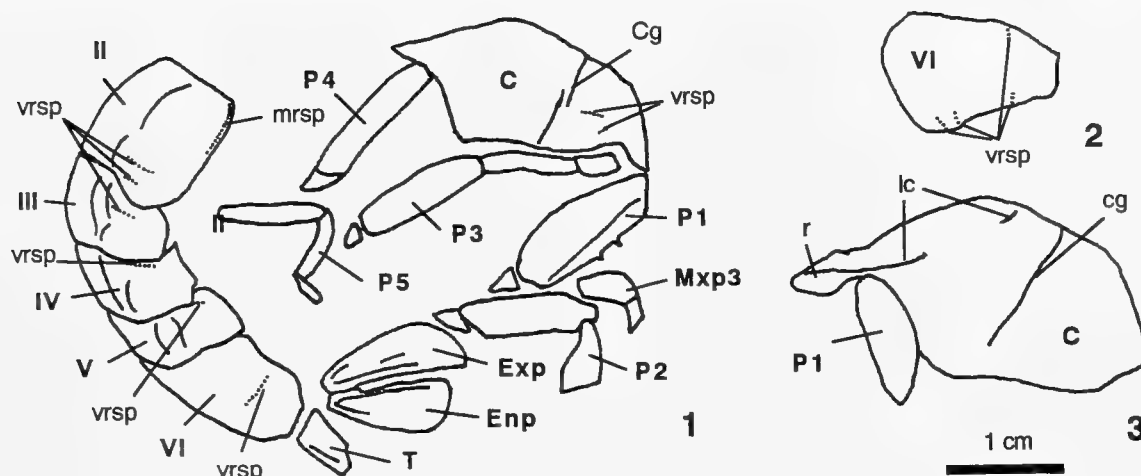


Figure 2. *Paki rurkonsimpu* gen. et sp. nov., MCM.A539 (holotype). 1. Carapace, abdominal somites, telson, uropod and pereopods, right lateral view. 2. Abdominal somite 6, dorsal view. 3. Carapace and pereopod 1, left lateral view. **Abbreviations:** C, carapace; cg, cervical groove; Enp, uropodal endopod; Exp, uropodal exopod; lc, lateral carina; mrsp, marginal row of setal pits; Mxp3, maxilliped 3; P1, pereopod 1; P2, pereopod 2; P3, pereopod 3; P4, pereopod 4; P5, pereopod 5; r, rostrum; T, telson; vrsp, vertical row of setal pits; II, abdominal somite 2; III, abdominal somite 3; IV, abdominal somite 4; V, abdominal somite 5; VI, abdominal somite 6.

Uropodal exopod triangular in outline, finely pitted dorsally, with weakly convex lateral margin and with diaeresis.

Chelae of pereopod 1 unknown. Some pereopods preserved, slender.

Discussion.—The species differs from *Hoploparia miyamotoi* Karasawa, 1998, the only known Japanese species from the Maastrichtian Izumi Group, by having the carapace with an antennal ridge and with well developed cervical and postcervical grooves. *H. kamuy* sp. nov. lacks well developed ridges between terga and pleura of abdominal somites, and marginal spines of pleura of abdominal somites 3–5.

Hoploparia kamuy sp. nov. is most similar to *Hoploparia pusilla* Secretan, 1964, from the Campanian of Madagascar, but differs in that the carapace bears a weak hepatic groove, a straight gastro-orbital groove, and a well defined prominence omega. *H. kamuy* sp. nov. resembles *Hoploparia arbei* Aguirre-Urreta, 1989 from the Puesto El Almo Formation (Turonian-Coniacian) of Argentina, but differs by absence of two tubercles on pleura of abdominal somites and of a granulated ridge on the branchial region.

Hoploparia kamuy represents the first record of the genus from the Turonian-Santonian of Japan.

Etymology.—The specific name is formed from 'kamuy', the name of a god in the Ainu language of Hokkaido.

Material examined.—MCM.A609 (holotype), Loc. YEZ-16, Oyubari, Yubari City; Upper Yezo Group (Lower Santonian;

Inoceramus amakusensis Zone by Ando and Kodama (1998)); collected by N. Nikkawa. MCM.A536 (paratype), Loc. YEZ-17, Ponbetsuzawa, Mikasa City; the basal part of the Upper Yezo Group (Upper Turonian; *Inoceramus teshioensis* Zone by Ando and Kodama (1998)); collected by S. Matsuda.

Infraorder Thalassinidea Latreille, 1831

Superfamily Axioidea Huxley, 1879

Family Micheleidae Sakai, 1992

Genus *Paki* gen. nov.

Type species.—*Paki rurkonsimpu* sp. nov. by monotypy.

Diagnosis.—Large-sized micheleid. Rostrum of carapace with rounded tip; lateral carina well developed; cervical groove distinct; *linea thalassinica* absent; anterolateral region with two vertical rows of setal pits anterior to cervical groove. Terga and pleura of abdominal somites 2–5 bounded by weak ridge; pleuron of somite 2 with two vertical rows of setal pits posteriorly and with marginal row of setal pits anteriorly; pleura of somites 3–6 with single vertical row of setal pits anteriorly; pleuron of somite 6 with two vertical rows of setal pits anteriorly and single vertical row of setal pits posteriorly. Telson rectangular with two longitudinal carinae. Uropodal exopod and endopod with median dorsal ridge and with convex margins.

Figure 1. 1, 2, 5, 6. *Hoploparia kamuy* sp. nov. 1. MCM.A536 (paratype), carapace, abdominal somites, telson and uropod, $\times 2.0$, right lateral view. 2. MCM.A609 (holotype), carapace and abdominal somites, $\times 2.0$, left lateral view. 5. MCM.A536 (paratype), abdominal somites and uropod, $\times 2.0$, left lateral view. 6. MCM.A609 (holotype), abdominal somites, $\times 2.0$, right lateral view. 3, 4, 7. *Paki rurkonsimpu* gen. et sp. nov. 3. MCM.A539 (holotype), carapace and eye stalks, $\times 3.0$, dorsal view. 4. MCM.A539 (holotype), carapace and left pereopod 1, $\times 3.0$, left lateral view. 7. MCM.A539 (holotype), carapace, abdominal somites, telson, uropod and pereopods, $\times 3.0$, right lateral view.

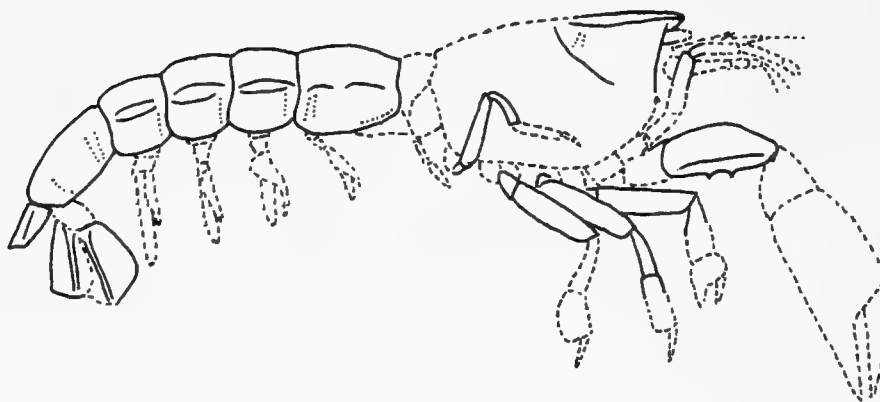


Figure 3. Reconstruction of *Paki rurkonsimpu* gen. et sp. nov.

Discussion.—The present new genus and species is assigned to the family Micheleidae Sakai, 1992 in the superfamily Axioidea Huxley, 1879 by lacking *linea thalassinica* on the carapace and by having rows of setal pits on the carapace and pleura of abdominal somites. According to Poore (1997) Micheleidae contains four Recent genera, *Michelea* Kensley and Heard, 1991, *Tethisa* Poore, 1994, *Meticonaxius* De Man, 1905 and *Marcusiaxius* Rodrigues and de Carvalho, 1972. The pattern of rows of setal pits on the anterior part of the carapace and the characters of propodi of pereopods 1–5 are not observed, but in the character of the remaining carapace and abdominal somites, the genus is most similar to *Meticonaxius* and *Marcusiaxius*. Two rows of pits anterior to the cervical groove on the carapace, two vertical rows of pits on the pleuron of abdominal somite 2, and rounded margins of the uropodal exopod and endopod readily distinguish the new genus from *Meticonaxius* and *Marcusiaxius*. *Paki* differs from *Tethisa* by having rows of setal pits on abdominal somites 3–5 and having an ovate uropodal exopod. The new genus also differs from *Michelea* in that the carapace bears a lateral carina and rows of pits in front of the cervical groove.

In the pattern of rows of setal pits on the abdominal somites *Upogebia rhacheochir* Stenzel, 1945 from the Turonian Britton Formation of Texas belongs to the family Micheleidae and may be assigned to *Meticonaxius* or *Marcusiaxius*. However, a well preserved carapace of Stenzel's species is needed to more precisely define the systematic position. Poore (1997: 364) described *Marcusiaxius* sp. from the Albian of Gault, Folkestone of England. Therefore, these occurrences extend the geologic range for the family Micheleidae back to the Cretaceous.

Etymology.—The generic name is derived from the word, 'paki', meaning shrimp in the Ainu language of Hokkaido; masculine gender.

***Paki rurkonsimpu* sp. nov.**

Figures 1.3, 1.4, 1.7; 2.1–2.3; 3

Description.—Large micheleid. Carapace laterally compressed. Anterior half of carapace poorly preserved. Rostrum extended anteriorly into rounded tip; dorsal surface missing. Eye stalks visible in dorsal view. Lateral carina well developed. Cervical groove distinct. *Linea thalassinica* absent. Anterolateral region with two vertical rows of setal pits anterior to cervical groove.

Abdominal somites 2–6 preserved. Somite 2 about 1.5 times as long as 3. Terga and pleura of somites 2–5 bounded by weak ridges. Pleuron of somite 2 with two vertical rows of setal pits posteriorly and with marginal row of setal pits anteriorly; pleura of somites 3–6 with single vertical row of setal pits anteriorly; pleuron of somite 6 reduced with two vertical rows of setal pits anteriorly and single vertical row of setal pits posteriorly. Surfaces of pleura of somites 2–5 finely punctuate. Telson rectangular, slightly wider than long, about 1/3 times as long as somite 6; lateral margin divergent posteriorly; dorsal surface with two longitudinal carinae and with two pits anteriorly. Uropodal exopod, lacking posterior half, with median dorsal ridge, convex anterolateral margin and finely serrated lateral margin. Uropodal endopod lacking anterior half, bearing median dorsal ridge and convex posterior margin.

Merus of pereopod 1 bearing convex lateral margin with longitudinal ridge and with two spines on ventral margin. Carpus and merus of pereopod 2 flattened. Propodus of pereopod 3 flattened; merus about 1.5 times as long as carpus. Merus of pereopod 4 ovate in cross section. Pereopod 5 short; merus about 1.5 times as long as carpus. Merus and carpus of maxilliped 3, slender, flattened laterally.

Discussion.—The species is similar to *Upogebia rhacheochir*, but differs by possessing two vertical and one marginal rows of setal pits on the pleuron of the abdominal somite 2.

Etymology.—The specific name is derived from the word 'rurkonsimpu', meaning a fairy living in seas in the Ainu language of Hokkaido.

Material examined.—MCM.A539 (holotype), Loc. YEZ-18, Kotanbetsu, Tomamae-cho, Tomamae-gun; Upper Yezo Group (Lower Campanian; *Sphenoceras orientalis* Zone);

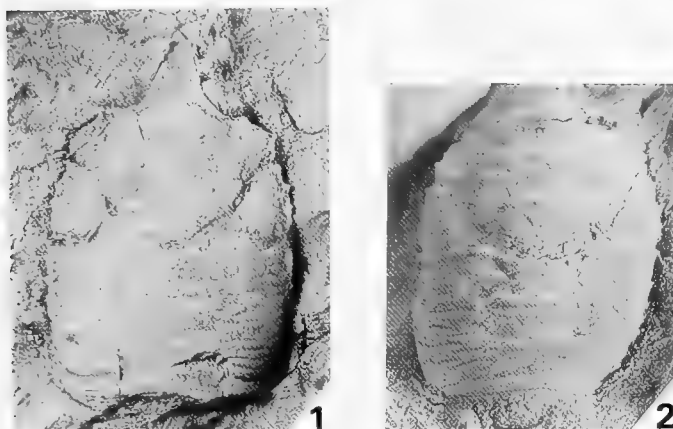


Figure 4. 1. *Luisogalathea tomitai* gen. et sp. nov., MFM247.010 (holotype), carapace, $\times 3.0$, dorsal view. 2. *Eomunidopsis kojimai* sp. nov., MFM247.011 (holotype), carapace, $\times 3.0$, dorsal view.

collected by H. Hayakawa.

Infraorder Anomala Boas, 1880
Superfamily Galatheaidea Samouelle, 1819
Family Galatheididae Samouelle, 1819
Genus ***Luisogalathea*** gen. nov.

Type species.—*Luisogalathea tomitai* sp. nov.

Diagnosis.—Moderate-sized galatheid. Carapace excluding rostrum, longer than wide, dorsally longitudinally gently convex. Rostrum triangular, simple, lacking lateral spines, concave dorsally; lateral margins smooth but bearing a small lateral projection on distal fifth. Lateral margin gently convex with small spines. Dorsal surface rugose without spines. Cervical and postcervical grooves well defined.

Discussion.—There may be, in the general outline of the carapace, similarity between *Luisogalathea* and the Tithonian-Maastrichtian genus, *Eomunidopsis* Via Boada, 1981, but absence of a median dorsal ridge on the rostrum and presence of spines on the lateral margin of the carapace readily distinguish *Luisogalathea* from *Eomunidopsis*. In *Eomunidopsis* supplementary dorsal furrows of the carapace are more or less developed.

Stenzel (1945) described two new galatheids, *Galathea cretacea* and *Galathea? limonitica* from the Pawpaw Shale (Albian-Cenomanian) of Texas. Bishop (1985) described *Eomunidopsis cobbani* Bishop, 1985 from the Campanian Larimer Sandstone of Colorado and assigned both of Stenzel's species to *Eomunidopsis*. Fraaye and Collins (1996: 323) suggested that these American species, *G. cretacea* and *E. cobbani*, having the rostrum without a median ridge, possibly belonged to *Paragalathea* Patruilius, 1959. *G. cretacea* differs from members of *Galathea* Fabricius, 1793 by having a triangular rostrum with smooth lateral margins. *Paragalathea* is characterised by having a large, broadly triangular rostrum and by having the dorsal surface of the carapace more or less tuberculate and with smooth lateral margins that diverge anteriorly. Both *G.*

cretacea and *E. cobbani* are transferred from *Eomunidopsis* to the present genus in that their carapaces have the genus characteristics of an acutely triangular rostrum with smooth lateral margins and without a median rostral ridge, a rugose dorsal surface, and gently convex lateral margins bearing spines. Only *Galathea? limonitica* belongs to the genus *Eomunidopsis* by exhibiting well defined carapace furrows.

Etymology.—The generic name is dedicated to the late Spanish paleocarcinologist, Dr. Luis Via Boada; feminine gender.

Species included.—*Luisogalathea tomitai* sp. nov., *Luisogalathea cobbani* (Bishop, 1985) comb. nov. from the Campanian-Maastrichtian of U.S.A., *Luisogalathea cretacea* (Stenzel, 1985) comb. nov. from the Cenomanian of U.S.A.

***Luisogalathea tomitai* sp. nov.**

Figure 4.1

Diagnosis.—Carapace excluding rostrum, subquadrate, dorsally longitudinally gently convex, width about 3/4 the length. Rostrum triangular, smooth dorsally with median depression; lateral margins bearing a small lateral projection on distal fifth. Orbital margin concave. Outer orbital angle weakly produced. Anterolateral angle with small spine. Lateral margin with 6 small spines. Orbitofrontal region depressed. Gastric, cardiac and branchial regions with transverse ridges and without spines. Cervical and epibranchial grooves well defined.

Description.—Carapace excluding rostrum, subquadrate in outline, dorsally longitudinally gently convex, width about 3/4 the length, greatest width about midlength. Rostrum triangular, gently downturned, about 1/4 as long as carapace width at the base, about 1/4 times as long as carapace length; dorsal surface smooth, with median depression; lateral margins smooth but bearing a small lateral projection on distal fifth. Orbital margin concave. Outer orbital angle weakly produced. Anterolateral angle with small spine. Lateral margin gently convex, bearing 6 small, forwardly di-

rected spines; 2 between cervical and epibranchial notches, and 4 posterior to epibranchial notch.

Orbitofrontal region depressed. Gastric region inflated; gently arched, raised edge between orbitofrontal and gastric regions; epigastric region ornamented with interrupted, transverse ridges, lacking spines, with shallow, median depression; proto- and mesogastric regions with 6 broadly rounded V-shaped ridges. Hepatic regions flattened. Cervical groove well defined, broad, deep. Cardiac region weakly marked, gently convex with 8 transverse ridges. Epibranchial regions inflated, separated from mesobranchial regions by deep postcervical grooves, ornamented with weak, transverse ridges. Other branchial regions densely decorated with interrupted transverse ridges.

Discussion.—*Luisogalatea tomitai* sp. nov. resembles *L. cretacea* (Stenzel) from the Pawpaw Shale (upper Albian) of Texas, but differs in having the rostrum with a smooth dorsal surface, the outer orbital angle with a weak projection, and the gastric, cardiac and branchial regions with fine ridges.

Etymology.—From A. Tomita who collected the type specimen.

Material examined.—MFM247.010 (holotype), Loc. YEZ-19, Nakafutamatagawa, Haboro-cho, Tomamae-gun; Upper Yezo Group (Santonian; *Inoceramus amakusensis* Zone by Ueda *et al.* (1961)).

Genus *Eomunidopsis* Via Boada, 1981

Type species.—*Galathea navarrensis* Van Straelen, 1940 by original designation.

Diagnosis.—Céphalothorax allongé, portant des crêtes transversales saillantes. Régions délimitées par des sillons bien visibles. Rostre caractérisé par sa pointe tridentée, dépourvu de dentelure sur ses bords latéraux et orné d'une carène médiane (from Via Boada, 1982).

Eomunidopsis kojimai sp. nov.

Figure 4.2

Diagnosis.—Carapace excluding rostrum, subquadrate, slightly longer than wide, dorsal surface moderately convex longitudinally. Orbital margin slightly concave. Outer orbital angle not produced. Anterolateral angle with small spine. Lateral margin gently convex with 8 small spines. Gastric, cardiac, hepatic and branchial regions ornamented with transverse and/or oblique ridges. Cervical and postcervical grooves well defined.

Description.—Carapace excluding rostrum, subquadrate in outline, about 4/5 times as wide as long. Rostrum not preserved about 1/4 as long as carapace width at the base. Orbital margin slightly concave. Outer orbital angle not produced. Anterolateral angle with very small spine. Lateral margin gently convex, armed with 8 small, forwardly directed spines; 1 anterior to cervical notch, 4 between cervical and epibranchial notches, 3 behind epibranchial notch.

Dorsal surface moderately convex longitudinally. Orbital regions flattened. Gastric region inflated; epigastric region vaulted, broadly triangular with oblique anterior ridge, interrupted, transverse ridge and median ridge behind it; proto- and mesogastric regions with 2 transverse ridges, anterior

one extending to hepatic region, gently curved ridge behind anterior one; mesogastric region with 3 gently curved ridges behind posterior transverse ridge, anterior and posterior ones shorter than middle; protogastric region with a pair of oblique ridges behind anterior transverse ridge. Hepatic regions ornamented with short, oblique ridges anteriorly. Cervical groove deep, broad. Cardiac region poorly defined with 3 transverse ridges diminishing in length posteriorly. Epibranchial region with 5 irregular, oblique ridges. Postcervical groove distinct. Other branchial regions with interrupted transverse ridges.

Discussion.—*Eomunidopsis kojimai* sp. nov. has close affinity with *Eomunidopsis navarrensis* (Van Straelen, 1940) from the Cenomanian of Spain, but differs by the presence of spines on the lateral margins of the carapace, and by absence of granules and tubercles on ridges of the dorsal regions. Ridges of the dorsal regions in *E. kojimai* are coarser than those in *E. navarrensis*. The new species resembles *Eomunidopsis meerssensii* Collins, Fraaye and Jagt, 1995 from the Maastrichtian Maastricht Formation of the Netherlands. In *E. kojimai* ridges are transversely and obliquely arranged on the dorsal surface while in *E. meerssensii* transverse ridges cover the dorsal surface.

Eomunidopsis, earliest known from the Oxfordian (Fraaye and Collins, 1996), is recorded from the Tithonian of Austria and Bulgaria (Via Boada, 1982), from the Cenomanian of Spain (Via Boada, 1982), from the Albian-Cenomanian of U.S.A. (Bishop, 1985) and the Maastrichtian of the Netherlands (Collins, Fraaye and Jagt, 1995). The occurrence of *E. kojimai* indicates that the genus reached Japan by the Santonian.

Etymology.—From Mr. T. Kojima who collected the type specimen.

Material examined.—MFM247.011 (holotype), Loc. YEZ-20, Wakkauenbetsugawa, Nakagawa-cho, Teshio-gun; Nigorikawa Formation (Santonian), Upper Yezo Group (Osana *et al.*, 1960).

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Early Silurian (Llandoveryan) radiolarians from the Ise area of the Hida "Gaien" Belt, central Japan

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Abstract. A moderately well-preserved Llandoveryan (early Early Silurian) radiolarian fauna has been discovered from the Ise area of the Hida "Gaien" Belt, in Izumi Village, Fukui Prefecture, central Japan. This is the oldest known radiolarian fauna in Japan, and was recovered from calcareous nodules in the siliceous shale portion of a sedimentary sequence consisting of siliceous shale, alternating tuffaceous sandstone and shale, and tuffaceous sandstone. The fauna contains *Haplotaeniatum tegimentum*, *Syntagentactinia afflicta*, *S. excelsa*, *Oriundogutta* sp., *Inanihella* sp., *Auliela* sp., *Palaeoephippium*? sp., and *Orbiculopylorum* sp. This fauna is characterized by an abundance of species in the genera *Haplotaeniatum*, *Syntagentactinia* and *Oriundogutta*, and is comparable with the early to middle Llandoveryan *Haplotaeniatum tegimentum* Assemblage and its equivalents in the southern Urals, Germany, and Nevada. Seventeen species of radiolarians belonging to 12 genera were systematically investigated.

Key words: Hida "Gaien" Belt, Ise area, Llandoveryan, Radiolaria, Silurian

Introduction

An understanding of the biostratigraphy and taxonomy of Silurian and Devonian radiolarians has progressed remarkably in the past decade (e.g., Nazarov and Ormiston, 1993; Noble and Aitchison, 1995). Numerous late Early Silurian to Middle Devonian radiolarian studies have been published for Japan (e.g., Wakamatsu *et al.*, 1990; Furutani, 1990; Aitchison *et al.*, 1996; Umeda, 1998), Australia (e.g., Stratford and Aitchison, 1997; Aitchison *et al.*, 1999), the United States (Noble, 1994), the southern Urals (Amon *et al.*, 1995), westernmost China (Li, 1994), and Germany (Kießling and Tragelehn, 1994). Based on these radiolarian biostratigraphic studies, we can estimate the age of radiolarian-bearing rocks of this interval.

Ordovician to early Early Silurian radiolarian biostratigraphy has been outlined by Nazarov and Popov (1980), Nazarov (1988), and Nazarov and Ormiston (1993). In addition to these studies, conducted in Kazakhstan and the southern Urals by Nazarov and his collaborators, a large number of Ordovician radiolarians have been reported from Spitsbergen (Fortey and Holdsworth, 1971), Newfoundland (Bergström, 1979; Renz, 1990a), the United States (Dunham and Murphy, 1976; Renz, 1990a, b; Kozur *et al.*, 1996), Australia (Webby and Blom, 1986; Goto *et al.*, 1992; Umeda *et al.*, 1992; Iwata *et al.*, 1995), Estonia (Nazarov and Nylvak, 1983), the Baltic region (erratic boulders) (Eisenack, 1971; Górka, 1994), China (Wang, 1993; Li,

1995), and Scotland (Aitchison, 1998; Danelian and Clarkson, 1998). In contrast, besides Nazarov's works (Nazarov, 1998; Nazarov and Ormiston, 1993), only a few papers describing early Early Silurian (Llandoveryan) radiolarians were published before the mid-1990s (Rüst, 1892; Stürmer, 1951, 1952, 1966; Goodbody, 1986). More recently, Llandoveryan faunas have been described from the Cherry Spring Chert in Nevada (Noble *et al.*, 1997; Noble *et al.*, 1998), Dalarna, Sweden (Maletz and Reich, 1997), Cornwallis Island, Arctic Canada (MacDonald, 1998), and Germany (Noble *et al.*, 1998). These studies demonstrate that Llandoveryan radiolarians have a high biostratigraphic potential. Early Silurian radiolarians, however, are still insufficiently known. Additional collecting is needed to establish a biostratigraphy and provide information on the faunal composition for this time period.

We are now studying the lithostratigraphy and radiolarian biostratigraphy of the Hida "Gaien" (=marginal) Belt in order to understand its tectonic and paleobiogeographic history (Kurihara and Sashida, 1998). We fortuitously discovered Llandoveryan radiolarians in calcareous nodules from the siliceous shale part of the clastic and volcanoclastic sequence exposed in the Ise area of the westernmost part of the Hida "Gaien" Belt, in Izumi Village, Ohno County, Fukui Prefecture. This early Early Silurian radiolarian fauna is the oldest one known in Japan. In this paper, we discuss the age assignment of the radiolarian fauna and systematically describe 17 species which belong to 12 genera including

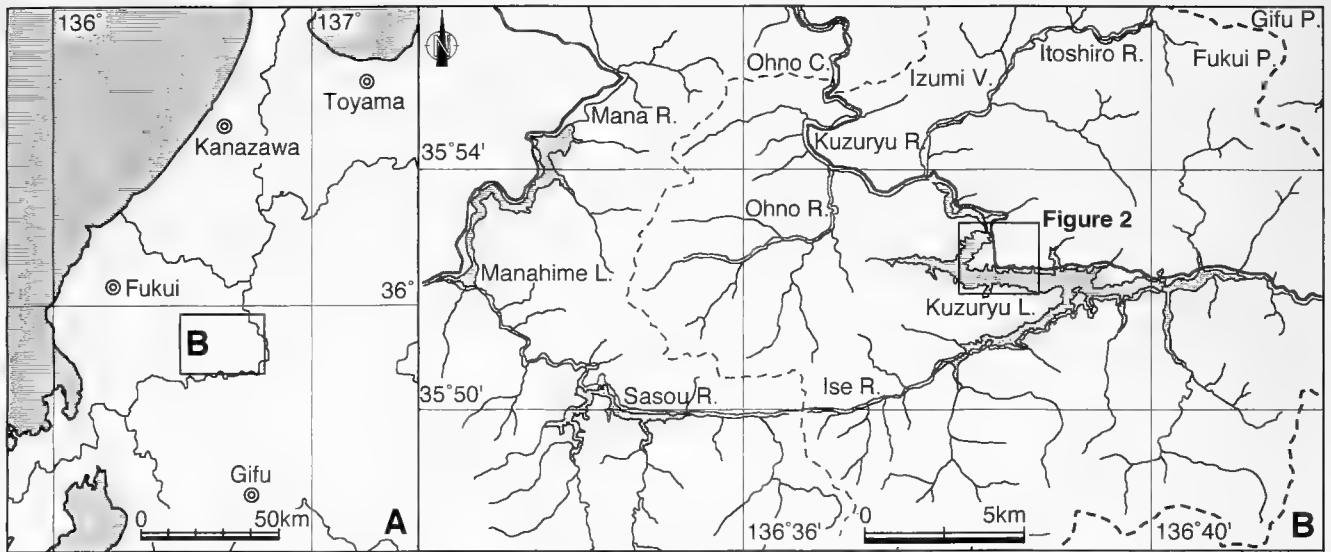


Figure 1. Index map showing the study area.

four undetermined genera.

Geologic setting

The Hida "Gaien" Belt, one of the most structurally complex areas in the Japanese geologic framework, occurs in a narrow area between the Hida and Mino Terranes. This belt is composed of weakly metamorphosed or unmetamorphosed Paleozoic and Mesozoic strata, including Ordovician to Devonian sediments, crystalline schists, and basic to ultrabasic rocks. Outcrops of these rocks can be found in the Omi-Renge, Fukuji, Moribu (Arakigawa), Naradani and Ise areas (e.g., Komatsu, 1990; Igo, 1990). The latter four of these five areas are covered by Middle Paleozoic strata and have been investigated by many workers (e.g., Tazawa *et al.*, 1997). Recent micropaleontological investigations of Ordovician strata show them to be fairly widely distributed in the Hitoegane district of the Fukuji area (Tsukada and Koike, 1996; Tsukada, 1997).

The Ise area, which extends from Izumi Village to Ohno City, Fukui Prefecture, is situated in the westernmost part of the Hida "Gaien" Belt. Its constituent rocks are exposed around Kuzuryu Lake and in the upper reaches of the Ise River to the Sasou-Mana River (Figure 1). The geology of this area has been studied by Kawai (1956), Kawai *et al.* (1957), Yamada (1967), and the Metal Agency of Japan (1980). Miyakawa and Yamada (1988) summarized the stratigraphy of the sedimentary rocks cropping out around Kuzuryu Lake, based on the studies of Yamada (1967) and Ohno *et al.* (1977). They subdivided these rocks into the following eight lithostratigraphic units, in ascending order: an unnamed Silurian unit, the Lower to Middle Devonian Kamianama Group, Middle Carboniferous Nagano Formation, Lower Permian Oboradani Formation, Middle Permian Nojiri Group and Magatoji Formation, post-Permian? Ohtani and Motodo Formations, and the Ashidani Group of unknown age. Among these litho-

stratigraphic units, the Nojiri Group, which is subdivided into the Oguradani Formation and overlying Konogidani Formation, crops out widely around Kuzuryu Lake. The other units, especially the Silurian and Devonian strata, complexly occur in narrow zones on the north side of Kuzuryu Lake and along the upper reaches of the Ise River.

Strata in this area contain rich Carboniferous and Permian fossils, including fusulinacians and corals in the Oboradani and Ohtani Formations, and brachiopods in the Oguradani Formation (e.g., Niko and Watanabe, 1987; Niko *et al.*, 1997; Tazawa and Matsumoto, 1998). The Devonian limestone of the Kamianama Group yields various kind of fossils (e.g., Hamada, 1959; Okazaki *et al.*, 1974; Kamiya and Niko, 1997) but no detailed paleontological study of them has been published. Recently, micropaleontological investigation by the present authors revealed the occurrence of Late Silurian to Middle Devonian radiolarians in the Kamianama Group (Kurihara and Sashida, 1998).

Lithology of the radiolarian-bearing rocks

The Early Silurian radiolarian-bearing calcareous nodules were collected from the siliceous shale portion of a sequence that consists of thin alternations of tuffaceous sandstone and shale, tuffaceous sandstone, and siliceous shale. The sequence crops out along a stream near the Kagero Tunnel, west of Nojiri, Izumi Village (Figure 2). Similar rocks are exposed in a roadcut east of the Anama Temple. These strata were previously assigned to the Konogidani Schalstein Formation (Ozaki *et al.*, 1954), the Tomedoro Schalstein "Member" [=Formation] (Kawai, 1956; Kawai *et al.*, 1957; Metal Agency of Japan, 1980), and the Permian Konogidani Formation (Yamada, 1967; Miyakawa and Yamada, 1988). Revision of the litho- and biostratigraphy in this area is needed (Kurihara, 1999).

In this stratigraphic section, the beds generally strike N25° to 35°W and dip 70° to 80°S (and sometimes almost verti-

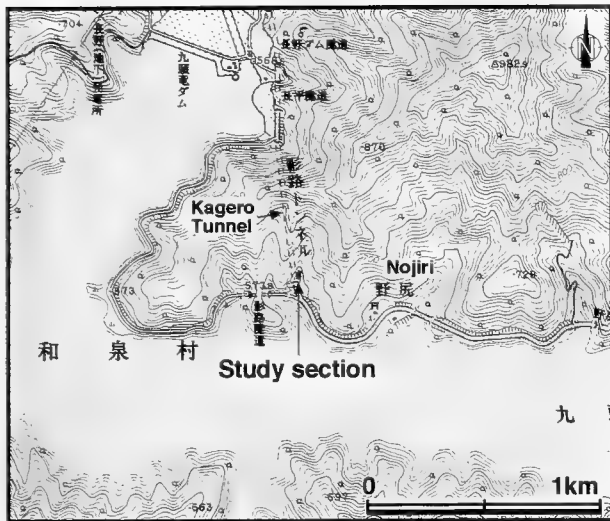


Figure 2. Locality map showing the location of the study section. Base map is after 1:25,000-scale topographic map of Japan, Quadrangle "Echizen-Asahi", Geographical Survey Institute of Japan.

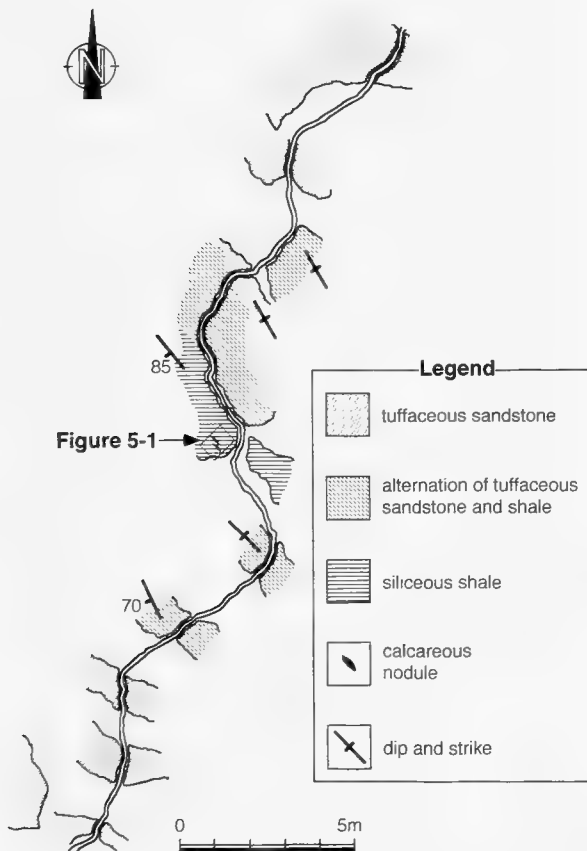


Figure 3. Route map along the study section.

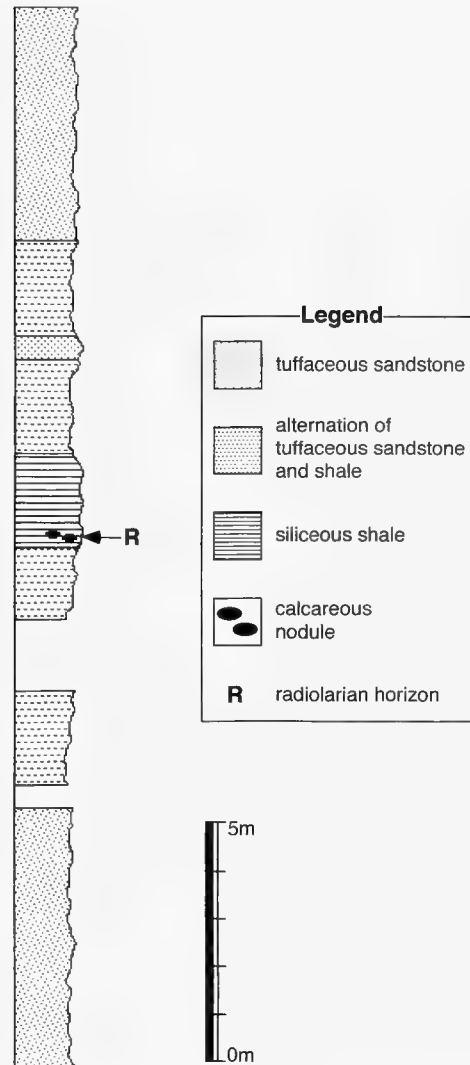


Figure 4. Column along the study section.

cally) (Figure 3). Although the stratigraphically highest structures were inaccessible in this section, we tentatively regard these rocks as a north-upward sequence, because sedimentary structures such as graded beddings indicating a north-upward orientation are observable at an outcrop east of the Anama Temple. The rock sequence of this section is as follows, in ascending order: tuffaceous sandstone (about 5.5 m); alternating tuffaceous sandstone and shale (about 4.5 m); siliceous shale (2 m); alternating tuffaceous sandstone and shale (4.5 m); and tuffaceous sandstone (5 m) (Figure 4). The tuffaceous sandstone is medium- to coarse-grained, massive and dark green to dark gray in color. The alternating tuffaceous sandstone and shale is thinly bedded and dark gray, gray, dark green, and black in color. Microscopic observation reveals that the sandstone layers are composed mainly of angular quartz fragments with a small amount of plagioclase and opaque minerals. The shale layers are partly similar to chert and contain very fine quartz grains in a muddy matrix with frequent thin lamina-

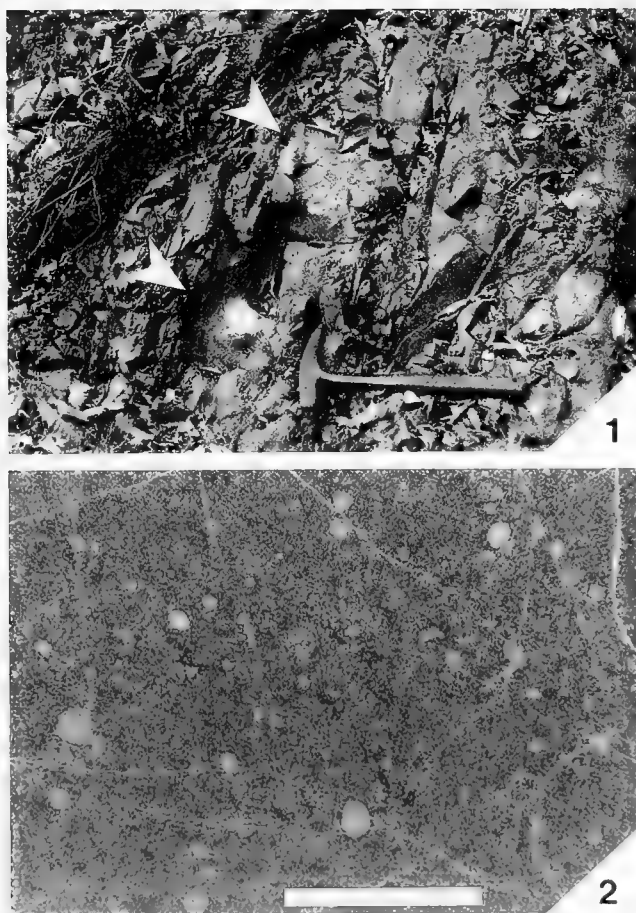


Figure 5. 1. Photograph showing the occurrence of radiolarian-bearing calcareous nodules (white arrows) in the study section (see Figure 3 for locality). 2. Photomicrograph of radiolarian-bearing calcareous nodule. Scale bar=1 mm.

tions of coarse quartz grains. The siliceous shale is dark gray and pale green in color and the thickness of each bed is 2 to 5 cm. In this exposure, the shale contains two calcareous nodules which are lenticular in shape and measure 15 cm and 6 cm in the major and minor axes, respectively (Figure 5.1). These nodules are hard, compact, dark gray in color and contain many radiolarian spheres. Radiolarian skeletons are scattered in a calcareous and muddy matrix, most are altered to calcite, and only their outlines formed of fine-grained quartz are preserved (Figure 5.2).

Method of extracting radiolarians

We collected calcareous nodules, siliceous shale, and the shaly part of the alternating tuffaceous sandstone and shale for radiolarian analysis. In order to extract radiolarians from the calcareous nodules, we soaked crushed rocks, each several centimeters in diameter, in a dilute acetic acid solution (5%) for 10 to 12 hours. For the siliceous rock samples, crushed rocks were soaked in a dilute hydrofluoric acid

Table 1. List of Llandoveryan radiolarians from the calcareous nodule.

HAPLENTACTINIIDAE

- Haplotaeniatum tegimentum* Nazarov & Ormiston
- Haplotaeniatum* sp. A
- Syntagentactinia afflicta* Nazarov & Ormiston
- Syntagentactinia excelsa* Nazarov & Ormiston
- Syntagentactinia* ? sp.

INANIGUTTIDAE

- Oriundogutta* sp.
- Oriundogutta* ? sp.
- Inanihella* sp.
- Inanihella* ? sp.
- Inaniguttidae gen. et sp. indet. sp. A

ANAKRUSIDAE

- Auliela* sp.

PALAEOSCENIDIIDAE

- Palaeoephippium* ? sp.

SPONGURIDAE

- Sponguridae gen. et sp. indet. sp. A

PYLENTONEMIDAE

- Cessipylorum* ? sp.

INCERTAE SEDIS

- Orbiculopylorum* sp.
- Spumellaria gen. et sp. indet. sp. A
- Spumellaria gen. et sp. indet. sp. B
- Spumellaria gen. et sp. indet.

(HF) solution (5 to 10%) for about 24 hours. The samples were washed and sieved through 270# nylon mesh. Radiolarians picked from the dried residues were coated with gold in a vacuum evaporator and observed with a scanning electron microscope. Other specimens were sealed on a slide glass and observed with a transmitted light microscope.

Radiolarian fauna and age

Radiolarians were recovered only from the calcareous nodules, and were absent in the siliceous shale and the shaly part of the alternating tuffaceous sandstone and shale. The identified radiolarians consist of 18 species belonging to 13 genera (Table 1). Radiolarians extracted from the calcareous nodules are generally poorly preserved, and unidentified spumellarian fragments are also numerous. This fauna is characterized by abundant species of the families Haplentactiniidae and Inaniguttidae, in association with Anakrusidae, Palaeoscenidiidae, Sponguridae, and Pylentonemidae. *Haplotaeniatum* and *Syntagentactinia*, in the family Haplentactiniidae, are common and are characterized by large, spherical, spongy, or concentric-layered shells. The following Haplentactiniidae species are present:

Haplotaeniatum tegimentum Nazarov and Ormiston, *Haplotaeniatum* sp. A, *Syntagentactinia afflicta* Nazarov and Ormiston, *Syntagentactinia excelsa* Nazarov and Ormiston, and *Syntagentactinia?* sp. Radiolarians of the family Inaniguttidae comprise the next most-dominant faunal component, including the following species: *Oriundogutta* sp., *Inanihella* sp., *Inanihella?* sp., and Inaniguttidae gen. et sp. indet. sp. A. Species in the families Palaeoscenidiidae and Sponguridae are less common, although *Palaeohippium?* sp. and Sponguridae gen. et sp. indet. sp. A are present. The following species were allocated to the families Anakrusidae, Pylentonemidae, and to incertae sedis; *Auliela* sp., *Cessipylorum?* sp., and *Orbiculopylorum* sp.

Silurian radiolarian biostratigraphy was first rationalized by Nazarov (1988) and Nazarov and Ormiston (1993), who proposed two radiolarian assemblages: the Early Silurian *Haplotaeniatum tegimentum* Assemblage and the Late Silurian *Inanihella tarangulica-Secuicollacta cassa* Assemblage. The *H. tegimentum* Assemblage, described from a middle Llandoveryan to Wenlockian siliceous rock sequence in the Sakmarsky Suite of the southern Urals, is characterized by *Haplotaeniatum labyrinthum* Nazarov and Ormiston, *H. cathenatum* Nazarov and Ormiston, *H. tegimentum* Nazarov and Ormiston, *Haplentactinia silurica* Nazarov and Ormiston, *Syntagentactinia excelsa* Nazarov and Ormiston, and *S. afflicta* Nazarov and Ormiston. As noted above, the present radiolarian fauna is characterized by species of *Haplotaeniatum* and *Syntagentactinia*, and therefore is referable to the *H. tegimentum* Assemblage of Nazarov (1988) and Nazarov and Ormiston (1993).

Noble *et al.* (1997) made a preliminary study of an early Llandoveryan radiolarian fauna in the Cherry Spring Chert of Nevada. They extracted from sulfide nodules a well-preserved radiolarian fauna consisting of abundant, large pylomate sphaerellarians identified as *Cessipylorum* (?) sp. A and *Cessipylorum* (?) sp. B, some rotasphaerids such as *Rotasphaera* sp. and *Secuicollacta* spp., and *Oriundogutta* sp. In addition, Noble *et al.* (1998) noted that the Nevada fauna described by Noble *et al.* (1997) contains abundant species of *Haplotaeniatum*. From the Frankenwald and Thuringia, Germany, Noble *et al.* (1998) also reported *Secuicollacta* spp. from black, organic-rich chert, the age of which is constrained by co-occurring graptolites as early Rhuddanian to early Telychian (early to late Llandoveryan). In the Main Valley, Germany, black chert gravel in Pleistocene river deposits contains well-preserved radiolarians, and was probably derived from the Frankenwald (Stürmer, 1951, 1952, 1966). Richter (1951) cited the age of this gravel as middle Rhuddanian to Aeronian (early to middle Llandoveryan), and Noble *et al.* (1998) identified the following species in it: *Syntagentactinia?* sp., *Orbiculopylorum adobensis* Noble, Braun and McClellan, *Orbiculopylorum* sp., and *Haplotaeniatum* sp.

Noble *et al.* (1997) pointed out the following characters of the Nevada fauna: (1) the species belonging to the family Inaniguttidae of the Wenlockian to Ludlowian, which have long and robust spines, are different from inaniguttids of the Nevada fauna. (2) Wenlockian to Ludlowian rotasphaerids commonly have six rods per spine unit and highly diversified spines such as grooved or bladed ones. In contrast,

rotasphaerid species in the Nevada fauna have five rods per spine unit and rod-shaped spines. (3) The Nevada fauna does not contain species in the families Palaeoscenidiidae and Ceratoikiscidae, which are notable taxa in Wenlockian faunas (Goodbody, 1986; Renz, 1988). Rotasphaerids have never been found in the present fauna, although their absence may be due in part to preservational bias, as these taxa are small and delicate. The morphological characters of the inaniguttids and the absence of ceratoikiscids are consistent with the work of Noble *et al.* (1997). The Nevada fauna also contains species of *Syntagentactinia* and *Haplotaeniatum*. In addition, large spherical radiolarians with the concentric and loosely spongy layers of the German fauna (Stürmer, 1951, 1952, 1966; Noble *et al.*, 1998) are very similar to the species of *Syntagentactinia* and *Haplotaeniatum* in the present fauna. Although *Orbiculopylorum* is rare, the present fauna is similar in its taxonomic composition to those in Nevada and Germany.

Nazarov and Ormiston (1993) inferred the age of the *H. tegimentum* Assemblage to be middle Llandoveryan to Wenlockian by showing that this assemblage occurs in a siliceous shale sequence that contains *Monograptus triangulatus* to *M. testis* zone graptolites. Noble *et al.* (1998) noted that the age of the *H. tegimentum* Assemblage is Rhuddanian (early Llandoveryan) to early Homeric (late Wenlockian) and that the lower range of this assemblage is consistent with the age of the Nevada and German faunas. However, they questioned the upper range of this assemblage, because the early to middle Llandoveryan radiolarian fauna is markedly different from the late Llandoveryan fauna. The late Llandoveryan faunas reported by Maletz and Reich (1997) and MacDonald (1998) lack large spongy spumellarians such as *Haplotaeniatum* and are characterized by the abundance of various taxa of rotasphaerids and entactiniids. According to Noble *et al.* (1998), the fauna from the middle Telychian (upper Llandoveryan) of Dalarna, Sweden contains *Haplotaeniatum* species but otherwise differs from the Nevada fauna in faunal composition. Therefore, as pointed out by Noble *et al.* (1998), the upper range of the *H. tegimentum* Assemblage does not extend above the Telychian, and possibly not above the Rhuddanian to Aeronian (early to middle Llandoveryan).

We cannot determine the precise age of the present fauna, but we assign it to the early to middle Llandoveryan, based on its similarity to the *H. tegimentum* Assemblage and to the Nevada and German faunas, as mentioned above.

Systematic paleontology

All specimens described in this paper are deposited in the Institute of Geoscience, University of Tsukuba (IGUT).

Order Polycystina Ehrenberg, 1838, emend. Riedel, 1967b

Suborder Spumellaria Ehrenberg, 1875

Family Haplentactiniidae Nazarov in Nazarov and Popov, 1980

Subfamily Haplentactiniinae Nazarov in Nazarov and Popov, 1980

Genus *Haplotaeniatum* Nazarov and Ormiston, 1993

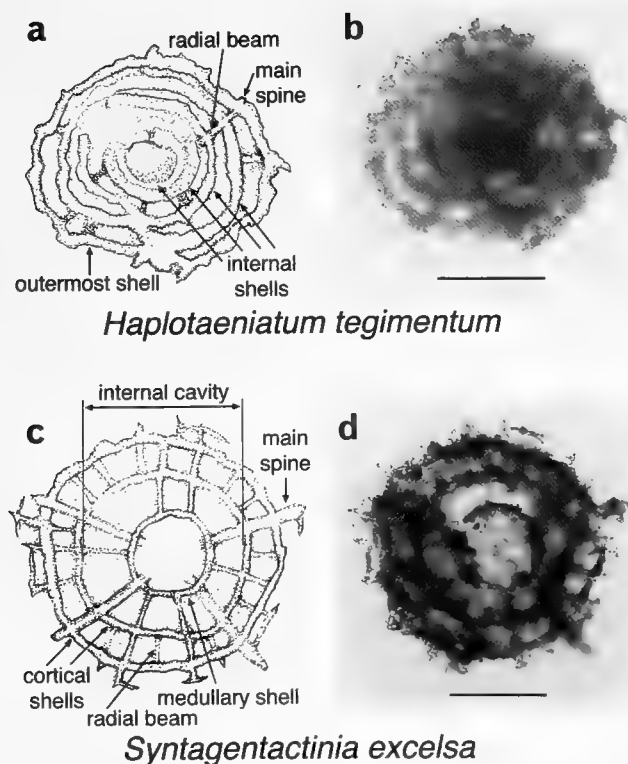


Figure 6. Schematic diagrams of skeletal structures and light transmission microphotographs of *Haplotaeniatum tegimentum* Nazarov and Ormiston (a, b) and *Syntagentactinia excelsa* Nazarov and Ormiston (c, d). Scale bars=100 μ m.

Type species.—*Haplotaeniatum labyrinthum* Nazarov and Ormiston, 1993.

Remarks.—Nazarov and Ormiston (1993) stated that the internal shells of this genus are interpreted as having formed by apophyses developed on the main spines. They also illustrated the schematic internal structure of this genus (Nazarov and Ormiston, 1993, text-figure 8b) and emphasized an important role of the main spines on skeletal structure as the characteristic of the family Haplentactiniidae. However, no specimen has the entactiniid-like internal structure formed by the main spines and extremely eccentrically positioned innermost shell among the photos presented by Nazarov and Ormiston (1993, pl. 3, figs. 9–16). Therefore, the generic diagnosis concerning the main spine by Nazarov and Ormiston (1993) is unconvincing, and the suprageneric classification of the genus *Haplotaeniatum* is problematic. We are not able to make an emendation for this genus owing to our poorly preserved material. However, the generic diagnosis and suprageneric classification of this genus will need to be revised on the basis of well-preserved material. In this paper, we follow the diagnosis presented by Nazarov and Ormiston (1993).

Haplotaeniatum tegimentum Nazarov
and Ormiston, 1993

Figure 7.1–7.13

Haplotaeniatum tegimentum Nazarov, 1988, p. 188, pl. 11, fig. 7 (nomen nudum); Nazarov and Ormiston, 1993, p.42, pl.3, figs. 14–16.

Description.—The external appearance of the shell is spherical, irregular spherical, or slightly elliptical. The outermost shell has many oval to irregularly rounded pores. In some specimens, a pylome-like oversized pore is present on the outermost shell surface (Figure 7.9–7.13). The inside of the outermost shell has an irregular spongy meshwork. The internal shells are spherical to subspherical, three to four in number, and concentrically arranged (Figure 6a, b). The innermost shell is often eccentrically positioned. Pores of the internal shells are circular to oval and differ in size. A small number of short, conical spines arise from the surface of the outermost shell. Under a transmitted light microscope, a radial beam (probably the main spine) penetrating the concentric internal shells and extending to the outermost shell is present (Figure 6a, b), but its detailed morphology is unclear owing to poor preservation. Short radial beams randomly arise from the outer surface of the internal shell. These beams connect the internal and outermost shells.

Measurements.—Based on 13 specimens, in μ m. Diameter of the outermost shell, 230–270, average, 250.

Remarks.—More than twenty specimens of this species were examined. According to the generic diagnosis of Nazarov and Ormiston (1993), this genus is characterized by having several concentric or spiral forms for the internal shells. A distinct spiral form was not observed in the present specimens, because the complex connections of the radial beams prevented us from appraising the inner structure of the shell. As shown in Figure 6a and 6b, several concentric internal shells are present. This species is distinguished from *Haplotaeniatum labyrinthum* Nazarov and Ormiston by having short, conical spines. *Haplotaeniatum cathenatum* Nazarov and Ormiston, which is characterized by having a large pylome, is similar to this species, especially to the above-described pylomate form. However, it is difficult to compare this species with *H. cathenatum*, because only one broken specimen of the latter species was illustrated by Nazarov (1988) and Nazarov and Ormiston (1993). *Haplotaeniatum? aperturatum* Noble, Braun and McClellan differs from the present species by having an irregular, spongy ball-like external shape and lacking a distinct internal shell.

Range and occurrence.—Middle to late Llandoveryan, southern Urals, southern Bashkiria and Northwestern Mugodzhari; Silurian, Cabriere, France; Llandoveryan, Ise area in the Hida "Gaigen" Belt.

***Haplotaeniatum* sp. A**

Figure 7.14–7.16

Description.—The shell is subspherical or slightly elliptical. The outermost shell has more than ten large circular to oval pores per hemisphere. The outermost shell bears no spines, but has small conical protuberances at the junction of intervening bars. The internal shell consisting of a loose lattice is subspherical, with large oval pores on its surface. Radial beams arise from the surface of the internal shell and connect the internal and cortical shells. These beams are

usually unbranched, but rarely bifurcate.

Measurements.—Based on three specimens, in μm . Diameter of the outermost shell, 230–270, average, 260.

Remarks.—This form is easily distinguished from other species of *Haploaeniatum* by having large circular to oval pores and the loose lattice to its internal shell. This species is similar to specimens of *Haploaeniatum primordialis*? (Rüst, 1892) described by Nazarov and Ormiston (1993). According to Nazarov and Ormiston (1993), the latter species is characterized by its smaller dimensions (194 to 208 μm) and a smaller number of internal shells. The present species differs from *H. primordialis*? (Rüst, 1892) by having a large diameter to the outermost shell.

Range and occurrence.—Llandoveryan, Ise area in the Hida "Gaien" Belt.

Genus ***Syntagentactinia*** Nazarov in Nazarov and Popov, 1980

Type species.—*Syntagentactinia biocculosa* Nazarov in Nazarov and Popov, 1980.

Syntagentactinia afflicta Nazarov and Ormiston, 1993

Figure 7.17, 7.18

Syntagentactinia afflicta Nazarov, 1988, pl. 11 fig. 6 (nomen nudum); Nazarov and Ormiston, 1993, p. 40, pl. 5, figs. 12, 13; Noble, Braun and McClellan, 1998, p. 723, fig. 5–2.

Description.—The shell of this species is composed of concentric cortical shells and a small medullary shell situated in the internal cavity. The cortical shells are spherical and two or three in number with long, robust, rod-shaped main spines. The main spines are commonly four in number and continuous into the medullary shell. In the interior of the medullary shell, however, the structure and emanation of the main spines are unclear. The diameter of the inner cortical shell is about two-thirds that of the outermost cortical shell. The surfaces of the outermost and inner cortical shells are irregularly perforated with oval to subangular pores. Many thin, radial beams connecting the outermost and inner cortical shells arise from the surface of the inner cortical shells. Due to being connected by many radial beams, the outermost and inner cortical shells form very complex sponge-like layers. Since only the broken medullary shell is preserved in our specimens, the detailed structure of the medullary shell is unclear. Based on observation with a transmitted light microscope, the diameter of the medullary shell is about one-third to one-fifth that of the outermost cortical shell.

Measurements.—Based on two specimens, in μm . Diameter of the outermost cortical shell, 280–300, average, 290; diameter of the inner cortical shell, 160–200, average, 180.

Remarks.—This species is easily distinguished from *Syntagentactinia excelsa* Nazarov and Ormiston by having long, robust main spines. Nazarov in Nazarov and Popov (1980) described *Syntagentactinia biocculosa* Nazarov and *Syntagentactinia pauca* Nazarov from the Middle Ordovician strata of eastern Kazakhstan. Nazarov's figures in Nazarov

and Popov (1980) of these Ordovician species are transmitted light photomicrographs, so it is difficult to compare Silurian species with Ordovician species in detail. Nazarov and Ormiston (1993), however, mentioned that *S. afflicta* is distinguished from Ordovician species by the clearly expressed internal half-closed shells and the development in the majority of specimens of two to four rather than six main spines.

Range and occurrence.—Early Llandoveryan, northern Adobe Range, Nevada; middle to late Llandoveryan, southern Urals, southern Bashkiria and Northern Mugodzhaz; Llandoveryan, Ise area in the Hida "Gaien" Belt.

Syntagentactinia excelsa Nazarov and Ormiston, 1993

Figures 7.19, 7.20; 8.1–8.7

Syntagentactinia excelsa Nazarov and Ormiston, 1993, p. 40, pl. 6, figs. 13, 14.

Description.—The external appearance of the cortical shell is spherical, subspherical, or elliptical, with thin rod-like main spines. The main spines are directly continuous into the internal portion of the shell (Figure 6c, d). The cortical shell is composed of two or three layers with irregular, three-dimensional meshwork. The surface of the cortical shell is irregularly porous and has small spines. The medullary shell, consisting of a spherical to irregularly shaped loose lattice, is placed in the internal cavity and has a diameter about 30 % that of the cortical shell diameter. The medullary and cortical shells are connected by short radial beams arising randomly from the surface of the medullary shell.

Measurements.—Based on five specimens, in μm . Diameter of the cortical shell, 200–270, average, 250; diameter of the medullary shell, 40–90, average, 70.

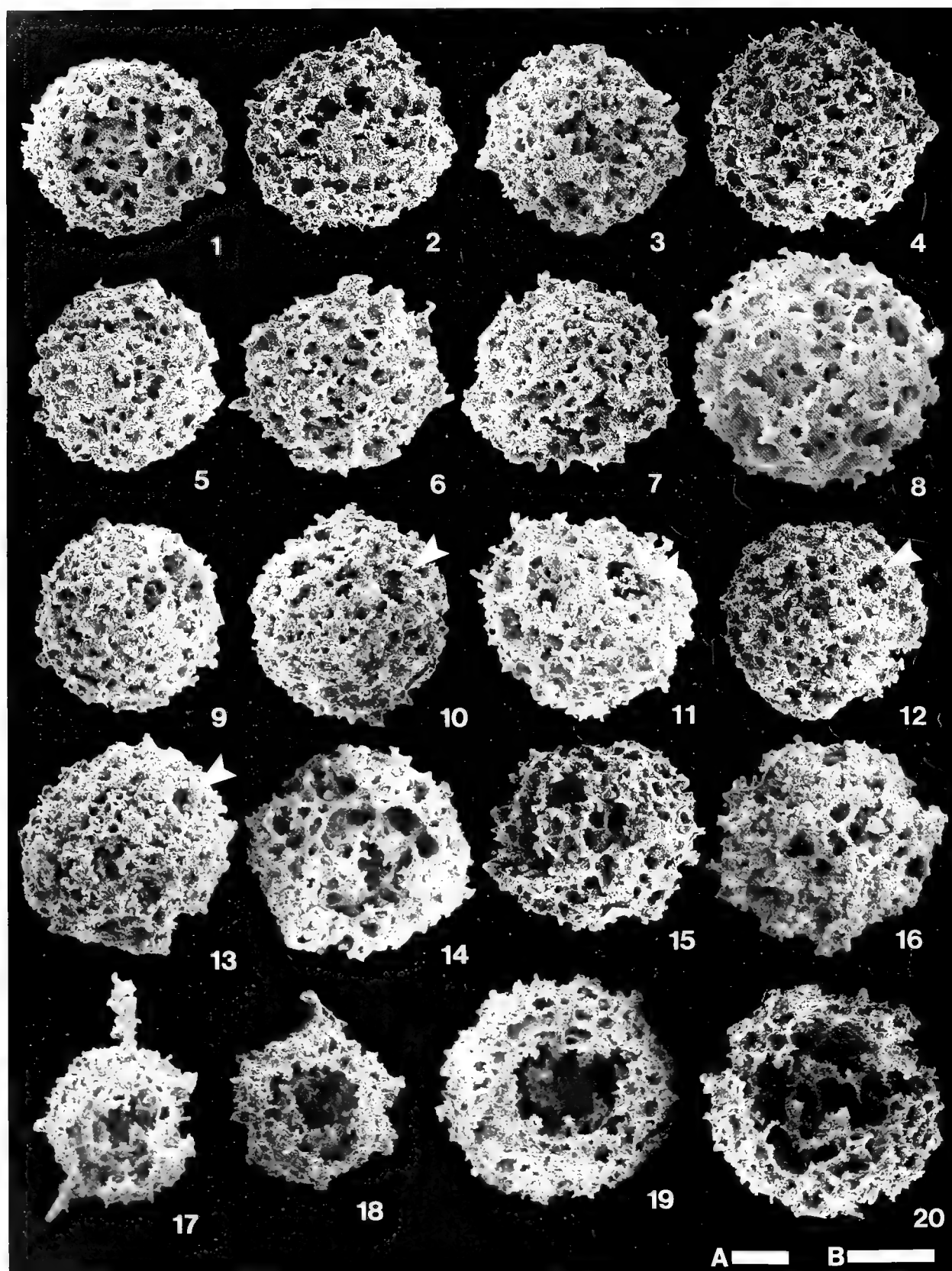
Remarks.—This species is distinguished from other species of this genus by having thin, weakly developed main spines. Some specimens of this species have a smaller cortical shell than that of *Syntagentactinia afflicta* described above. Although Nazarov and Ormiston (1993) suggested that this species has a peculiar eccentric position of the medullary shell, this characteristic is not clearly shown in their illustrated specimen (Nazarov and Ormiston, 1993, pl. 4, fig. 13). The shell constitution of this species is similar to that of *Syntagentactinia*? sp. illustrated by Noble *et al.* (1998) from chert gravel of the Main Valley, Germany. However, *Syntagentactinia*? sp. of Noble *et al.* (1998) has a large diameter of the cortical shell, up to 700 μm . *Syntagentactinia* sp. A of Noble *et al.* (1998) is similar to the present species, but differs from *S. excelsa* by having a distinctly latticed medullary shell.

Range and occurrence.—Middle to late Llandoveryan, southern Urals, southern Bashkiria and Northwestern Mugodzhaz; Llandoveryan, Ise area in the Hida "Gaien" Belt.

***Syntagentactinia*? sp.**

Figure 8.8

Remarks.—Only one poorly preserved specimen was obtained. The shell of this species is composed of an irregu-



larly fine spongy layer having three thick main spines. This spongy layer may be a product of the state of preservation. This species is similar to *Syntagentactinia*? sp. of Noble *et al.* (1998), except that it has a rather small shell diameter. Although its detailed shell structure has not yet been examined, we tentatively include this form in *Syntagentactinia*.

Range and occurrence.—Llandoveryan, Ise area in the Hida "Gaien" Belt.

Family Inaniguttidae Nazarov and Ormiston, 1984,
emend. Noble, 1994

Genus *Oriundogutta* Nazarov, 1988

Type species.—*Astroentactinia ramificans* Nazarov, 1975.

Oriundogutta sp.

Figure 8.9–8.15

?*Oriundogutta* sp. Noble, Ketner and McClellan, 1997, pl. 1, figs. 7, 8.

Description.—The thick, spherical cortical shell is single and latticed with 10 to 15 external spines per hemisphere. The external spines are short, conical to rod-like and taper distally. Five to six main spines arising from the surface of the medullary shell in each hemisphere are long and have one or two short by-spines. The pores of the latticed shell are circular, and oval to irregularly circular in shape. Thick and broad pore frames are pentagonal or hexagonal in shape. The medullary shell is small, latticed and polyhedral to spherical in shape. The pores of the medullary shell are circular to oval and larger than those of the cortical shell. The pore frames of the medullary shell are thinner than those of the cortical shell. SEM and transmitted light microscopic observations show the absence of an internal spicule in the interior of the medullary shell.

Measurements.—Based on five specimens, in μm . Diameter of the cortical shell, 150–300, average, 210; diameter of the medullary shell, 60–110, average, 90.

Remarks.—More than twenty specimens of this species were examined and they bear diagnostic characters of the *Oriundogutta*: one porous, thick cortical shell, a polyhedral to spherical medullary shell, and more than eight external spines. It is distinguished from other species of this genus by having short, conical to rod-like external spines and a smaller number of these spines. ?*Oriundogutta* sp., reported by Noble *et al.* (1997) from the lower Llandoveryan of Nevada, is exceedingly similar to this species in external shape.

Range and occurrence.—Early Llandoveryan, northern Adobe Range, Nevada; Llandoveryan, Ise area in the Hida "Gaien" Belt.

Oriundogutta? sp.

Figure 8.16–8.20

Remarks.—The cortical shell of this species is spherical and has three to four sturdy, rod-like main spines per hemisphere. Some of the examined specimens have several thin, needle-like spines. The external shell features of *Oriundogutta*? sp. are similar to those of *Oriundogutta ramificans* (Nazarov), except that the former's main spines are smaller in number. This species is distinguished from *Oriundogutta* sp. by having a finely perforated cortical shell and thin pore frames. The internal shell structure cannot be observed, so the generic position of this species is tentative.

Range and occurrence.—Llandoveryan, Ise area in the Hida "Gaien" Belt.

Genus *Inanihella* Nazarov and Ormiston, 1984,
emend. Noble, 1994

Type species.—*Helioentactinia bakanasensis* Nazarov, 1975.

Inanihella sp.

Figure 9.1–9.4

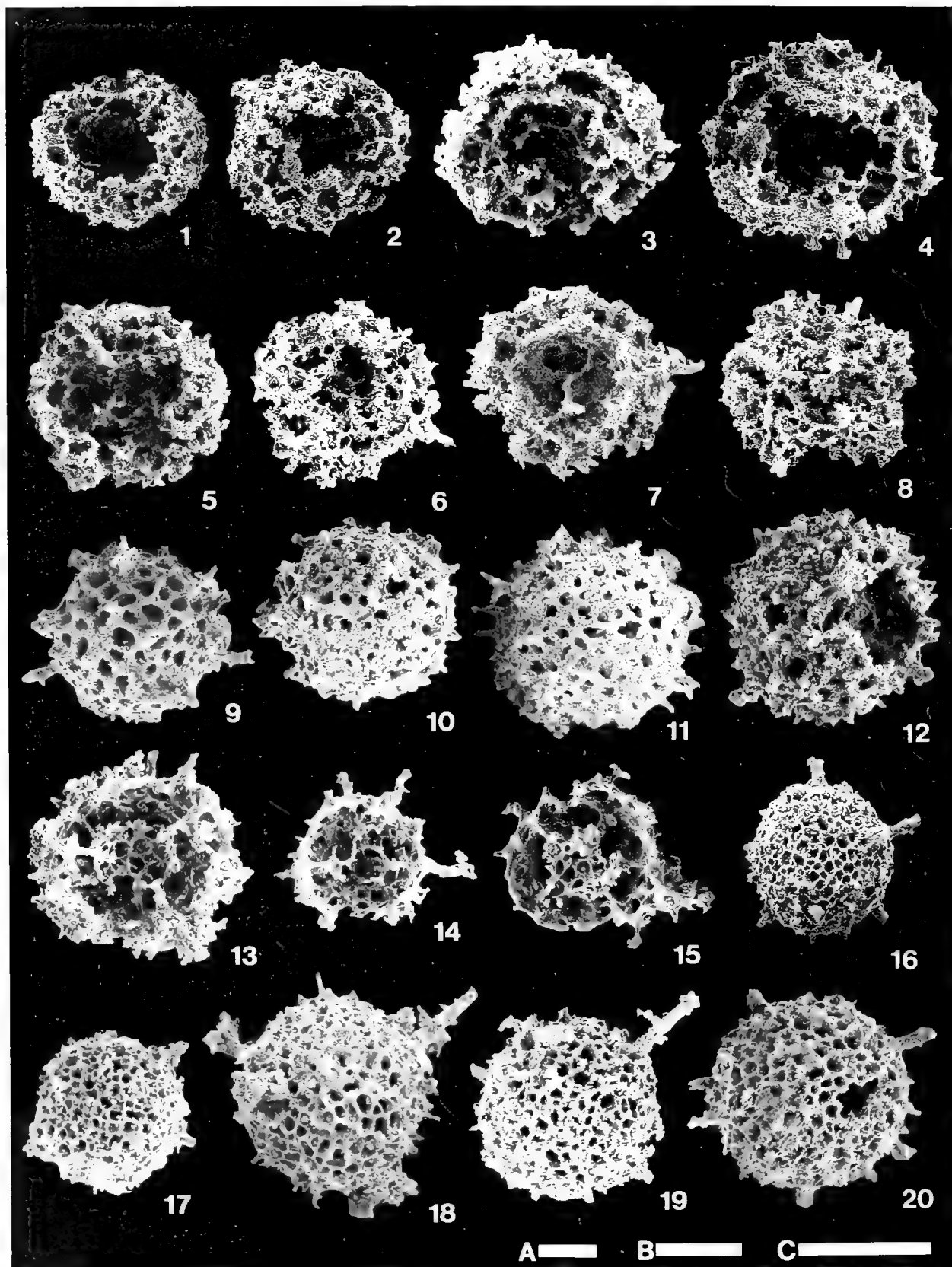
Description.—The shell of this species is composed of two latticed cortical shells with more than four main spines per hemisphere. The inner cortical shell is spherical and has circular to oval pores with pentagonal to hexagonal pore frames. The outer cortical shell is delicate and irregularly perforated. Several short, needle-like spines arise from the surface of the outer cortical shell. The inner and outer cortical shells are connected by many thin radial beams. Based on observations with a transmitted light microscope, the internal shell is single, and probably latticed, but its detailed structure has not been observed. The main spines are thin, rod-like and taper gently toward the distal end.

Measurements.—Based on four specimens, in μm . Diameter of inner cortical shell, 190–220, average, 200; diameter of outer cortical shell, 260–300, average, 280; maximum length of spine, 70.

Remarks.—This species is characterized by the presence of two cortical shells, yet no specimens were found that perfectly preserve the delicate outer cortical shell. The present form has a spine morphology similar to *Inanihella bakanasensis* (Nazarov) reported from the Middle Ordovician of Kazakhstan by Nazarov (1975).

Range and occurrence.—Llandoveryan, Ise area in the Hida "Gaien" Belt.

Figure 7. 1–13. *Haplotaeniatum tegimentum* Nazarov and Ormiston, 1: IGUT-TK 863, 2: IGUT-TK 816, 3: IGUT-TK 874, 4: IGUT-TK 894, 5: IGUT-TK 782, 6: IGUT-TK 858, 7: IGUT-TK 875, 8: IGUT-TK 958, 9: IGUT-TK 860, 10: IGUT-TK 783, 11: IGUT-TK 794, 12: IGUT-TK 884, 13: IGUT-TK 776. White arrows of 9 to 13 indicate a pylome-like oversized pore. 14–16. *Haplotaeniatum* sp. A, 14: IGUT-TK 866, 15: IGUT-TK 873, 16: IGUT-TK 801. 17, 18. *Syntagentactinia afflicta* Nazarov and Ormiston, 17: IGUT-TK 897, 18: IGUT-TK 824. 19, 20. *Syntagentactinia excelsa* Nazarov and Ormiston, 19: IGUT-TK 817, 20: IGUT-TK 747. Scale bars A and B each equal 100 μm ; A applies to 15, 17, 18, B to 1–14, 16, 19, 20.



Inanihella? sp.

Figure 9.5–9.7

Remarks.—The basic skeleton of this species is composed of a porous inner cortical shell with traces of delicate outer cortical shell. The internal shell structure has not yet been observed. Three or four rod-like main spines are present on the inner cortical shell per hemisphere. Many short conical spines arise from the junction of the pore frame of the inner cortical shell. The inner cortical shell and main spines of this species are very similar to those of the *Inanihella* sp. described above. Although only traces of the delicate outer cortical shell are present, we tentatively include this form in *Inanihella*.

Range and occurrence.—Llandoveryan, Ise area in the Hida "Gaien" Belt.

Inaniguttidae gen. et sp. indet. sp. A

Figure 9.8, 9.9

Remarks.—Several poorly preserved specimens were examined. This species is characterized by a large, spherical cortical shell with an oversized pore. This pylome-like pore is circular in shape and has no lip on its surrounding pore frame. The external shell morphology is somewhat similar to the *Oriundogutta* sp. herein. We tentatively include this species in the family Inaniguttidae. A larger sample of this species is needed in order to determine its generic position.

Range and occurrence.—Llandoveryan, Ise area in the Hida "Gaien" Belt.

Family Anakrusidae Nazarov, 1977

Genus *Auliela* Nazarov, 1977*Type species.*—*Auliela aspersa* Nazarov, 1977.*Auliela* sp.

Figure 9.10

Description.—The shell is spherical, with more than one hundred spines arising from the hemisphere. The spines are straight, cylindrical and taper gently toward the distal end. Most of these spines are short or broken, owing to poor preservation, but some attain 60 µm in length. There are no pores on the shell surface. The internal structure is unknown.

Measurements.—Based on one specimen, in µm. Diameter of shell, 300; maximum length of spine, 60.

Remarks.—Only one specimen of this species was examined. Our specimen has a spherical shell with numerous cylindrical spines. This character and the external shape indicate assignment to the genus *Auliela*. *Auliela aspersa* Nazarov, the type species of this genus, described from the

Middle Ordovician of eastern Kazakhstan by Nazarov (1977), is similar to the present species. The spines of *A. aspersa* Nazarov are described as being hollow, but the present specimen has mostly solid spines. This difference may be attributed to the development of secondary deposits of silica and poor preservation. This species, however, differs from *A. aspersa* Nazarov in having a rather smaller shell and shorter spines. *Auliela taplowensis* Webby and Blom, described from the Upper Ordovician of eastern Australia by Webby and Blom (1986), differs from this species by having longer spines and a smaller shell diameter.

Range and occurrence.—Llandoveryan, Ise area in the Hida "Gaien" Belt.

Family Palaeoscenediidae Riedel, 1967a, emend.

Holdsworth, 1977; Goodbody, 1982;

Furutani, 1983; Goodbody, 1986

Genus *Palaeoehippium* Goodbody, 1986

Type species.—*Palaeoehippium bifurcum* Goodbody, 1986.

Palaeoehippium? sp.

Figure 9.11–9.13

Remarks.—Completely preserved specimens of this species have not yet been obtained. The basic skeleton of this species probably consists of a six-rayed form. The spines arising from each ends of a short medium bar are rod-like, gently tapered toward the distal end. Among these spines, three (probably four) spines have two or three rather thin secondary spines at the midpoint of their length, and the other spines lack the branched spines. *Palaeoehippium tricornis* Goodbody, described from the Cape Phillips Formation of the Canadian Arctic Archipelago by Goodbody (1986), has indistinguishable apical and basal spines and is similar to this species. Furthermore, this species has a resemblance to *Haplentactinia arrhinia* Foreman, 1963 in having a six-rayed basic spicule. However, the former species differs from the latter by having branches arising at one level along some spines and lacking an irregularly latticed shell. In this paper, we tentatively assign this species to the genus *Palaeoehippium*, considering its similarity to *P. tricornis*.

Range and occurrence.—Llandoveryan, Ise area in the Hida "Gaien" Belt.

Family Sponguridae Haeckel, 1887, emend.

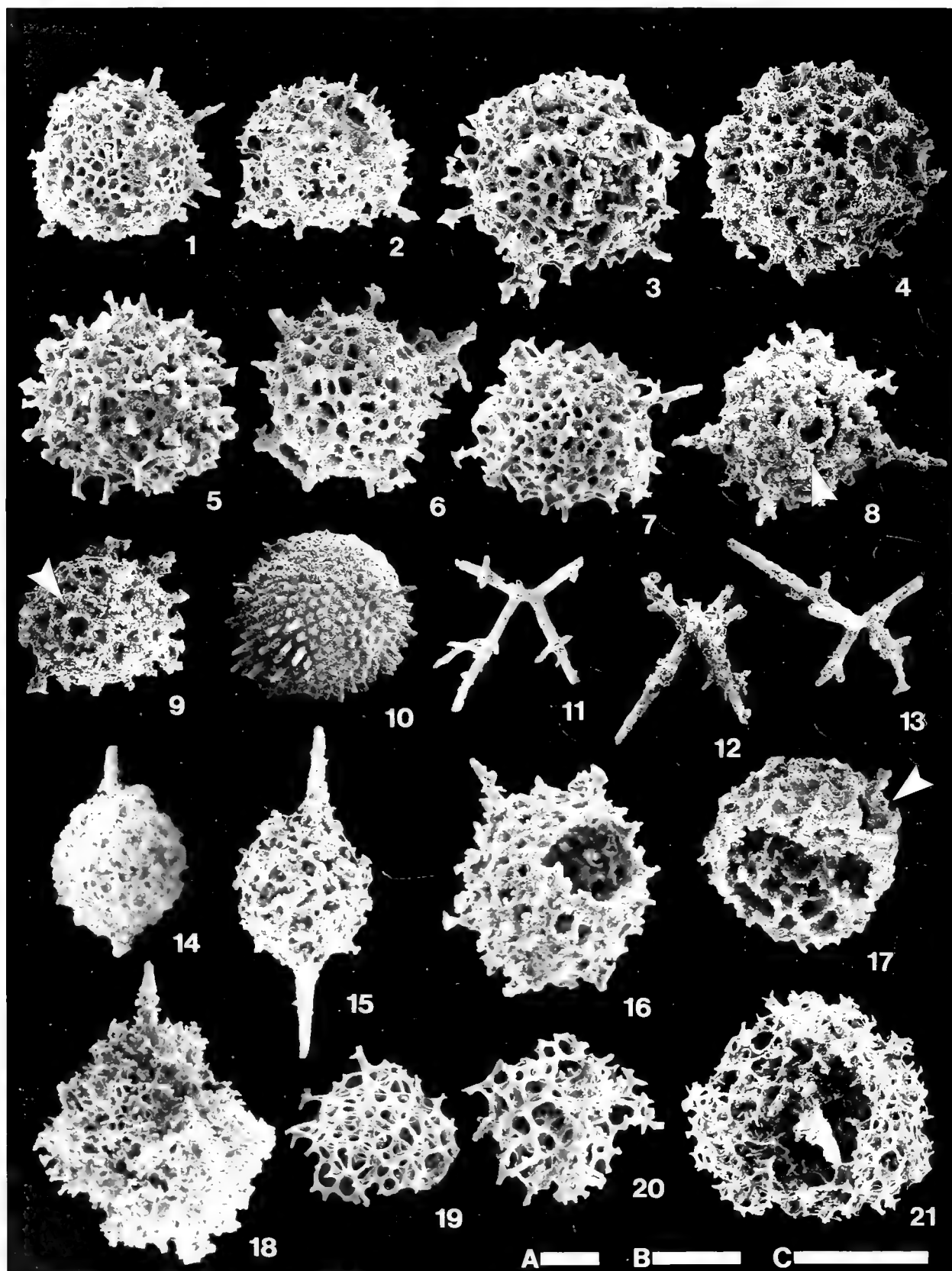
Pessagno, 1973

Sponguridae gen. et sp. indet. sp. A

Figure 9.14, 9.15

Description.—The shell is elliptical, with two polar main

Figure 8. 1–7. *Syntagentactinia excelsa* Nazarov and Ormiston, 1: IGUT-TK 723, 2: IGUT-TK 836, 3: IGUT-TK 961, 4: IGUT-TK 864, 5: IGUT-TK 724, 6: IGUT-TK 822, 7: IGUT-TK 766. 8. *Syntagentactinia?* sp., IGUT-TK 899. 9–15. *Oriundogutta* sp., 9: IGUT-TK 859, 10: IGUT-TK 895, 11: IGUT-TK 819, 12: IGUT-TK 879, 13: IGUT-TK 901, 14: IGUT-TK 761, 15: IGUT-TK 850. 16–20. *Oriundogutta* ? sp., 16: IGUT-TK 892, 17: IGUT-TK 931, 18: IGUT-TK 845, 19: IGUT-TK 865, 20: IGUT-TK 919. Scale bars A, B and C each equal 100µm; A applies to 1, 8, 16, 17, B to 2–7, 9–11, 13–15, 18–20, C to 12.



spines. These spines are rod-like, strongly tapered, and identical in length and thickness. The proximal portions of the spines are weakly bladed. The surface of the outer shell has many circular to polygonal pores of irregular size. The interior of the shell consists of a loose, irregular spongy meshwork. The distinctly layered internal structure was not observed.

Measurements.—Based on one specimen, in μm . Length of major axis of shell, 190; length of minor axis of shell, 150; length of spines, 100.

Remarks.—Several poorly preserved specimens of this species were examined. Although the internal structure of the multiple concentric spongy layers is unknown, this form is characterized by an elliptical spongy shell and polar main spines, and is included in the family Sponguridae. Noble (1994) has recognized Late Silurian genera (*Pseudospongoprimum* Wakamatsu, Sugiyama and Furutani, 1990, and *Devoniglausus* Wakamatsu, Sugiyama and Furutani, 1990) of the family Sponguridae. The species assigned to *Pseudospongoprimum* by Noble (1994) are especially characterized by a subspherical to elliptical spongy shell with polar main spines, and they are similar to the present species. This unidentified species, however, differs from all species of *Pseudospongoprimum* by having a loose spongy meshwork and equal lengths to the polar main spines. The exact identification of this species is postponed until sufficient specimens have been examined.

Range and occurrence.—Llandoveryan, Ise area in the Hida "Gaien" Belt.

Family Pylentonemidae? Deflandre, 1963

Genus *Cessipylorum* Nazarov in Afanas'eva, 1986

Type species.—*Pylentonema insueta* Nazarov in Nazarov, Popov and Apollonov, 1975.

Remarks.—Nazarov and Ormiston (1993) tentatively placed the genera *Cessipylorum* and *Aciferopylorum* Nazarov and Ormiston, 1993 in the family Pylentonemidae Deflandre. We tentatively follow that placement.

Cessipylorum? sp.

Figure 9.16

Remarks.—Only one specimen was examined. The cortical shell is subspherical and irregularly porous, and bears a large circular aperture. The pore frame around the aperture is slightly turned up and has small conical spines. The presence of a medullary shell and an inner structure is unclear. The other species in *Cessipylorum*, such as *Cessipylorum apertum* (Nazarov), have long, robust main spines, but this species has only a few thin and short spines. The

generic placement of this species is tentative.

Range and occurrence.—Llandoveryan, Ise area in the Hida "Gaien" Belt.

Family Incertae sedis

Genus *Orbiculopylorum* Noble, Braun and McClellan, 1998

Type species.—*Orbiculopylorum marginatum* Noble, Braun and McClellan, 1998.

Orbiculopylorum sp.

Figure 9.17

Remarks.—The illustrated specimen is distinguished by a prominent pylome on the cortical shell. The cortical shell is thick and probably perforated. However, the detailed structure of the cortical shell cannot be observed, owing to poor preservation. The pylome is circular and flanged. The medullary shell consists of a loose lattice and is irregularly spherical and centrally located. This species is similar to *Orbiculopylorum adobensis* Noble, Braun and McClellan, described from the Cherry Spring Chert of Nevada by Noble *et al.* (1998). However, the former species differs from the latter by having a less compact medullary shell.

Range and occurrence.—Llandoveryan, Ise area in the Hida "Gaien" Belt.

Spumellaria gen. et sp. indet. sp. A

Figure 9.19, 9.20

Labyrinthine spumellarian Noble, Ketner and McClellan, 1997, pl. 1, fig. 14.

Description.—The shell consists of a spongy, three-dimensional meshwork and is irregularly spherical. The spongy meshwork is loose, delicate and has no regular structure or layering. The exterior meshwork seems to be looser than that in the interior. The pores framed by the looped, loose, spongy meshwork are circular to elliptical and vary in size. On the external surface of the shell, short subconical to cylindrical spines arise from the pore frame and usually bifurcate, or rarely trifurcate, at their distal end.

Measurements.—Based on two specimens, in μm . Diameter of shell, 120–170, average, 145.

Remarks.—This species is characterized by an irregular spongy shell without layering. A form referable to this species has been reported by Noble *et al.* (1997) as Labyrinthine spumellarian. *Haplotaeniatum fenestratum* Goto, Umeda and Ishiga, described from the Upper

Figure 9. 1–4. *Inanihella* sp., 1: IGUT-TK 973, 2: IGUT-TK 976, 3: IGUT-TK 986, 4: IGUT-TK 893. 5–7. *Inanihella?* sp., 5: IGUT-TK 975, 6: IGUT-TK 855, 7: IGUT-TK 937. 8, 9. *Inaniguttidae* gen. et sp. indet. sp. A, 8: IGUT-TK 956, 9: IGUT-TK 808. White arrows of 8 and 9 indicate an oversized pore. 10. *Auliela* sp., IGUT-TK 732. 11–13. *Palaeoephippium?* sp., 11: IGUT-TK 843, 12: IGUT-TK 737, 13: IGUT-TK 842. 14, 15. Sponguridae gen. et sp. indet. sp. A, 14: IGUT-TK 940, 15: IGUT-TK 827. 16. *Cessipylorum?* sp., IGUT-TK 922. 17. *Orbiculopylorum* sp., IGUT-TK 743. White arrow of 17 indicates a pylome. 18. Spumellaria gen. et sp. indet., IGUT-TK 972. 19, 20. Spumellaria gen. et sp. indet. sp. A, 19: IGUT-TK 725, 20: IGUT-TK 851. 21. Spumellaria gen. et sp. indet. sp. B, IGUT-TK 868. Scale bars A, B and C each equal 100 μm ; A applies to 1, 2, 8, 10, 14, 18, B to 3–7, 9, 11–13, 15–17, 19, 21, C to 20.

Ordovician of eastern Australia by Goto *et al.* (1992), is similar to this species in the basic construction of its spongy shell. However, *H. fenestratum* lacks certain diagnostic characteristics of *Haplotaeniatum*, such as concentric layers or a spiral form. The taxonomic placement of this species will depend on finding additional specimens.

Range and occurrence.—Early Llandoveryan, northern Adobe Range, Nevada; Llandoveryan, Ise area in the Hida "Gaien" Belt.

Spumellaria gen. et sp. indet. sp. B

Figure 9.21

Remarks.—Several broken specimens were obtained. The illustrated specimen has a spherical shell consisting of a spongy, three-dimensional meshwork. The spongy meshwork structure of this species is similar to that of *Spumellaria* gen. et sp. indet. sp. A, described above, but differs from the latter by having an internal cavity.

Range and occurrence.—Llandoveryan, Ise area in the Hida "Gaien" Belt.

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行 事 予 定

- ◎第150回例会は、2001年1月27日(土)と28日(日)に「茨城県自然博物館」で開催されます。シンポジウム案の申し込み締切日は2000年4月末日、個人講演の申し込み締切日は2000年12月1日(金)です。
- ◎2001年年会・総会は、21世紀最初の年会ですので、「21世紀の古生物学」を統一テーマとし、東京地区でシンポジウムを中心とした形式で、将来計画委員会が中心となって開催を企画することが決定しております。開催の案内や形式については「化石」67号、83-84頁をご覧ください。
- ◎第151回例会(2002年1月下旬開催予定)の開催申し込みは、今のところありません。
- ◎2002年年会・総会(2002年6月下旬開催予定)には福井県立博物館から開催申し込みがありました。
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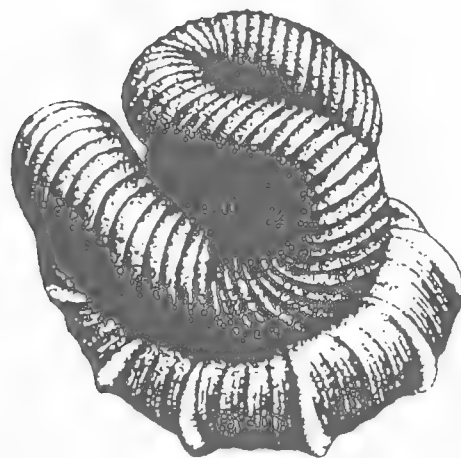
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Cover: Idealized sketch of *Nipponites mirabilis* Yabe, a Late Cretaceous (Turonian) nostoceratid ammonite. Various reconstructions of the mode of life of this species have been proposed, because of its curiously meandering shell form (after T. Okamoto, 1988).

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The presence of an azhdarchid pterosaur in the Cretaceous of Japan

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Abstract. An incomplete pterosaur cervical vertebra from the “Upper” Formation (Late Cenomanian–Early Turonian) of the Mifune Group, Kumamoto Prefecture, Japan, is described. Although not complete, this vertebra is very elongated and has a reduced neural spine, allowing its assignment to the Azhdarchidae. It differs from other azhdarchids by being less constricted and by the morphology of the postzygapophyses. This Japanese occurrence extends the distribution of the Azhdarchidae during the Cretaceous to the easternmost part of Asia.

Key words: Azhdarchidae, Late Cretaceous, Mifune Group, Pterosauria, Southwest Japan

Introduction

The occurrence of pterosaur remains in Japan is very limited. The first record of these volant archosaurs in Japan was the distal part of a femur and other associated bones that were found in Cretaceous sediments of Hokkaido (Obata *et al.*, 1972). Since then, a limited number of fragmentary material has been recovered from a few localities. These include an incomplete wing phalanx (Okazaki and Kitamura, 1996) and the proximal articulation of a left wing metacarpal (Ikegami and Tamura, 1996) both found in the “Upper” Formation of the Mifune Group, in Kumamoto Prefecture, an incomplete wing phalanx (Unwin *et al.*, 1996), and an incomplete cervical vertebra (Chitoku, 1996). To these we add the description of an incomplete cervical vertebra that can be referred to the Azhdarchidae, a long-necked pterodactyloid. The occurrence of this specimen was previously reported (Ikegami, 1997), and a full description and comparison of this material are presented here.

Geological setting

The pterosaur fossil described here was recovered from an outcrop near Amagimi dam, Mifune Town, Kamimashiki-gun, Kumamoto Prefecture, Japan (Figure 1), which is located approximately 20 km southeast of central Kumamoto City. The Mifune Group, broadly distributed in this area, was named by Matsumoto (1939), and was subdivided into three formations, namely the “Basal”, “Lower”, and “Upper”

Formations (Figure 2). Although the terms basal, lower, and upper should not be used for formation names, those names were given as official names by Matsumoto (1939) and have not been revised since then. Therefore, these terms are used here until a full revision is published. Tamura and Sawamura (1964), Tamura and Tashiro (1966), and Tamura (1970, 1976, 1977, 1979) further investigated and expanded the distribution of the group, and studied the pelecypod fauna from those strata. The stratigraphy of the group, however, has not markedly changed from the original study of Matsumoto (1939).

The “Upper” Formation is characterized by red mudstone, blue-green sandstone, and more than dozen tuff beds (Matsumoto, 1939). It reaches 800 to 1000 m in thickness, and vertebrate fossils have been found in several horizons (Tamura *et al.*, 1991).

The azhdarchid specimen described here was found in a coarse sandstone bed, about 30 cm thick and with muddy patches, which belongs to the middle part of the “Upper” Formation (Figure 2). This coarse sandstone is more or less lens-shaped, and appears at a distinct level between two tuff beds. The locality of the azhdarchid, as well as other sites from the same horizon, also yielded many fragmentary bones of various taxa, including dinosaurs, crocodiles, turtles, fishes, and mammals (Tamura *et al.*, 1991; Hirayama, 1998; Setoguchi *et al.*, 1999).

The “Upper” Formation is considered terrestrial based on the rock facies and fossil taxa. Although those fossils do not include taxa that are useful for identifying the age of the

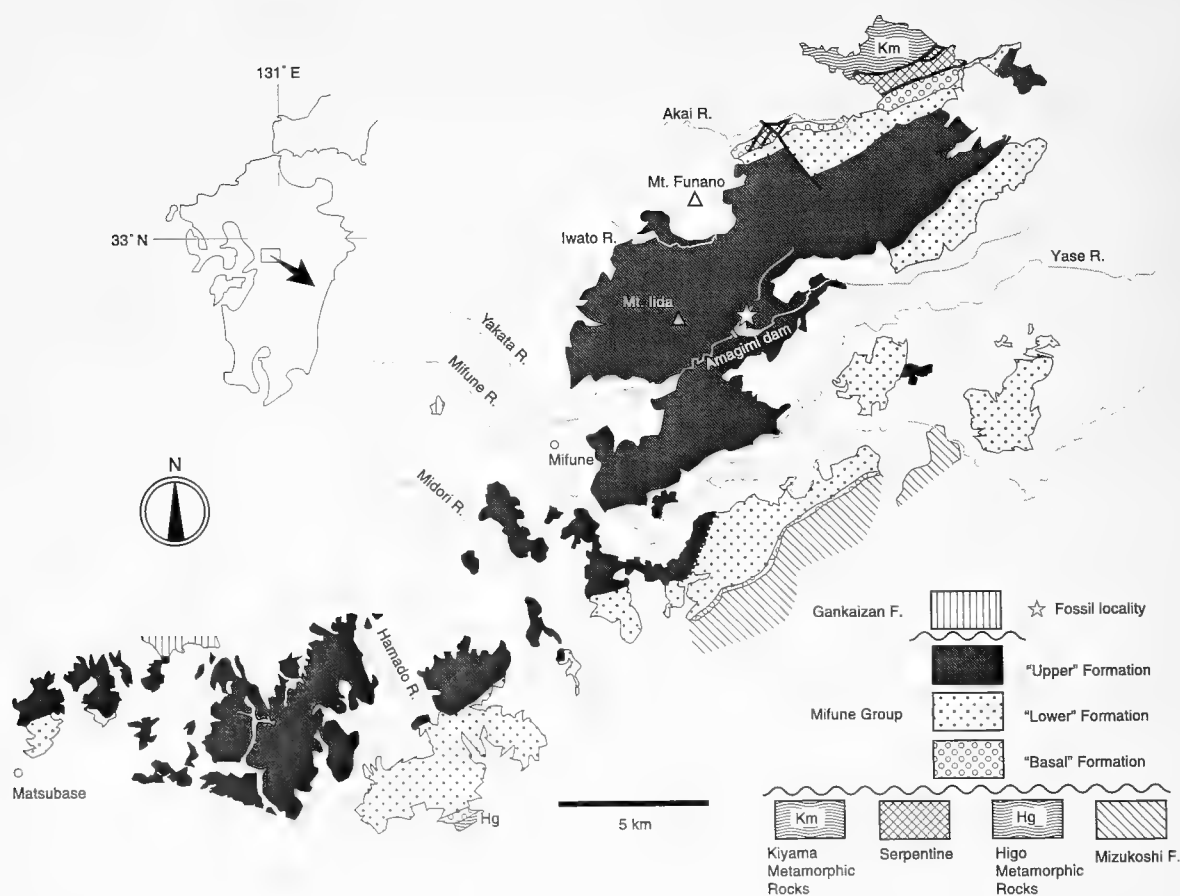


Figure 1. Geological map of the area southeast of Kumamoto City (after Tamura, 1979), showing the locality of the azhdarchid pterosaur.

formation, *Eucalycoceras* sp. cf. *E. spathi* is known from the middle part of the "Lower" Formation, suggesting a middle Cenomanian age for this unit (Tamura and Matsumura, 1974). However, the Gankaizan Formation that overlies the "Upper" Formation, south of Kumamoto City, yielded *Inoceramus amakusensis*, which indicates the early Santonian (Tamura and Tashiro, 1966). These specimens suggest that the age of the "Upper" Formation lies between middle Cenomanian and early Santonian. However, the lower part of the Ohnogawa Group, which outcrops east-northeast of the Mifune Group, includes red beds and tuff beds that resemble the "Upper" Formation of the Mifune Group. The upper marine facies of the Ohnogawa Group has yielded *Inoceramus hobetsuensis*, indicating middle Turonian age (Noda, 1969). Therefore, the age of the "Upper" Formation of the Mifune Group can be estimated as late Cenomanian to early Turonian (Matsumoto *et al.*, 1982). Hirayama (1998) also suggested as the age of the "Upper" Formation late Cenomanian to early Turonian, based on the similarity between chelonian assemblages from this formation and those of Central Asia.

Systematic description

Family Azhdarchidae Nessov, 1984
Azhdarchidae gen. et sp. indet.

Figure 3

Material.—MDM (Mifune Dinosaur Museum) 349, a cervical vertebra from the Mifune Group; a cast in Museu Nacional, Rio de Janeiro (MN 5022-V).

Description.—The specimen consists of an incomplete procoelous cervical vertebra, with the cranial part including the prezygapophyses missing (Fig. 3). The vertebra is compressed dorsoventrally, which causes distortion towards the left lateral side. Although this compression changed the natural shape of this bone, it is not completely flattened like many pterosaur specimens from the Niobrara Chalk of North America, but maintains some of its original three-dimensionality. Several breaks, cutting the vertebral body and some filled with matrix, are present, particularly on the dorsal surface (Figure 3 A, B). On the ventral side, the cortical bone is crushed, forming several bony plates in a "broken eggshell"-like pattern.

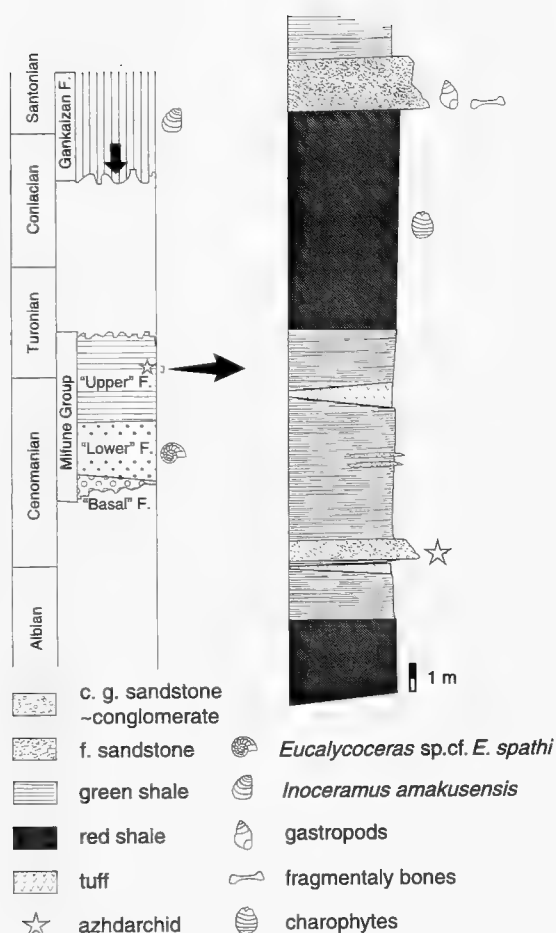


Figure 2. Stratigraphy of the Upper Cretaceous sediments in the area southeast of Kumamoto City (after Tamura and Matsumura, 1973; Tamura and Tashiro, 1966; Matsumoto *et al.*, 1982) on the left, and columnar section of the "Upper" Formation of the Mifune Group at the fossil locality on the right.

Near the caudal articulation, the neural spine is broken, but the preserved parts suggest that it was very low. Slightly away from the articulation, this structure almost disappears, being reduced to a very thin ridge that extends for most of the preserved vertebral length. On the right side, another ridge runs parallel to the neural spine, about 5 mm away from the midline. Evidence of a similar ridge is also observed about 6 mm from the midline on the left side, most of which was lost during the compaction of the specimen. This ridge is interpreted as the transverse process that, in this specimen, is very reduced and does not reach the postzygapophysis.

The postzygapophyses are set well apart from the vertebral body, with the left one better preserved. They are not parallel to each other, and each of them forms an estimated angle with the midline of the centrum of about 33° (based on the right side) in dorsal view.

Also in distal view, the postzygapophyses are set apart

from the vertebral body, although the angle relative to the ventral surface is very difficult to estimate (Figure 3 G,H).

The articular surface of the postzygapophysis is suboval; the dorsal part is constricted, and the ventral part is rounded. Above the dorsal margin, a small process is present.

The posterior condyle is not very well preserved in this specimen. Apparently, it had a suboval outline, with the major axis directed lateromedially. The dorsal margin is rounded, and the ventral margin is flattened. On each side of the condyle, the postexpophyses are observed, of which the left side is better preserved. It forms a small process that is directed laterocaudally.

Two pneumatic openings are observed lateral to the neural canal; the right one is better preserved. Both pneumatic openings are slightly smaller than the neural canal and occupy a relatively high position in the posterior surface of the vertebra. There is no evidence of a third pneumatic foramen above the neural canal.

The reconstruction of the middle part for this cervical vertebra indicates that the transverse section was oval and slightly wider than high (see Table 1). Based on the preserved part, this vertebra was very elongate, with a minimum length/width ratio of 4.3, but likely over 5. The exact length, however, is unknown.

Comparisons and discussion.— Comparisons of this specimen with other pterosaur cervical vertebrae show that it shares one feature with the Azhdarchidae: its relative length. Elongated mid-cervical vertebra with a low neural spine is one of the synapomorphies of azhdarchids (Howse, 1986), indicating that this specimen represents a member of this pterosaur clade. Padian (1984, 1986) refined the diagnosis of Nessov (1984), showing among other things that the vertebra centrum enclosed the neural canal, a situation nearly unique in vertebrates.

As far as comparisons are possible, this cervical vertebra shows some differences from other azhdarchids. In dorsal view, the postzygapophyses are thinner and set apart at a greater angle relative to the vertebra's midline, as compared to *Quetzalcoatlus* sp. (Howse, 1986) and to *Azhdarcho* (Nessov, 1984; cast MN 4692-V). The position of the pneumatic foramina lateral to the neural canal is similar to the condition in *Quetzalcoatlus* (TMM 42422-24, cast MN 4699-V), and also of *Azhdarcho*. In the cranial articulation of some cervical vertebrae attributed to the latter, there is an extra pneumatic opening above the neural canal (Nessov, 1984). Whether a similar opening was present in the Japanese specimen is unknown.

This specimen further differs from all known azhdarchids by having a well developed ridge parallel to the neural spine, by being less constricted with comparatively straighter lateral margins, and by having the process above the postzygapophyses smaller but comparatively more pointed.

So far, only two azhdarchids with a complete or nearly complete neck are known: *Quetzalcoatlus* sp. from the USA and *Zhejiangopterus linhaiensis* from China. The former, unfortunately, is still undescribed. The latter was originally regarded as a nyctosaurid (Cai and Wei, 1994), but Unwin and Lü (1997) reclassified this taxon in the Azhdarchidae, based on the low position of the orbit relative to the nasoantorbital fenestra, which is an azhdarchid

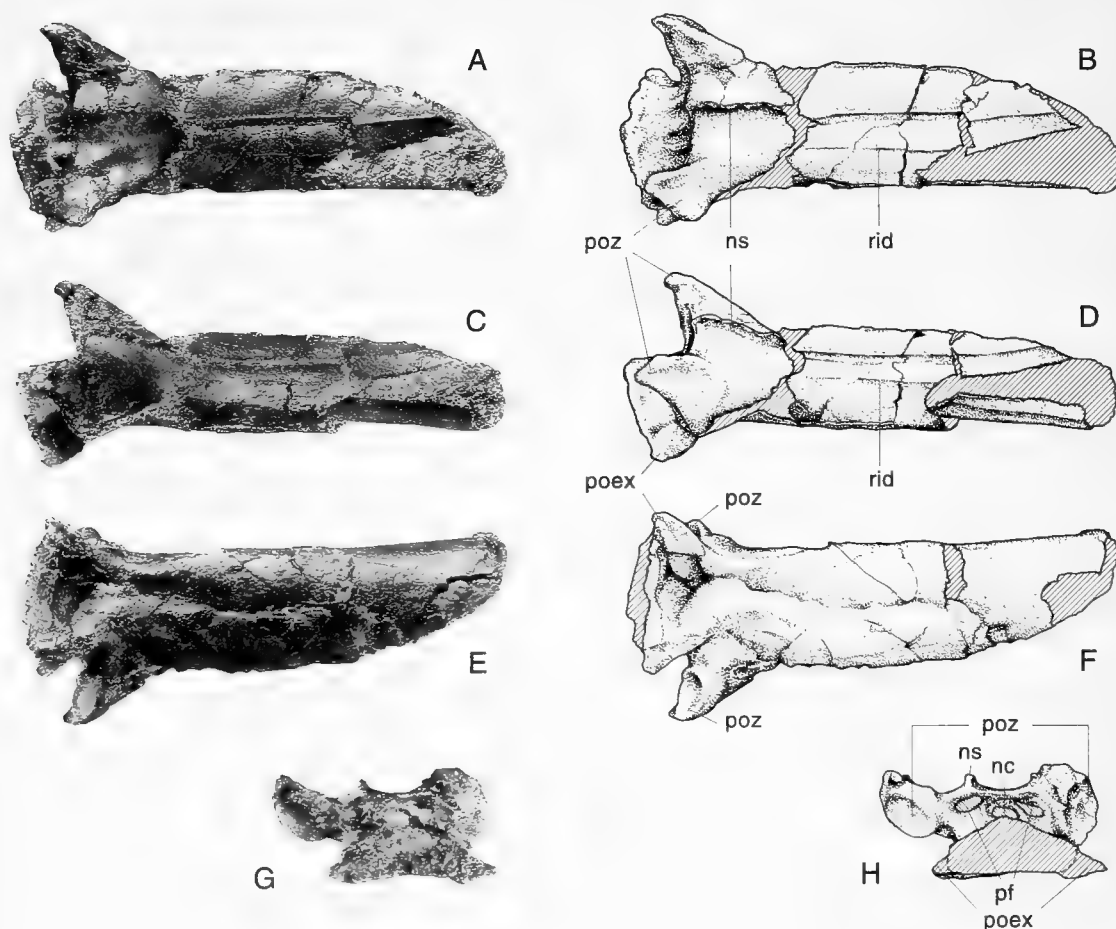


Figure 3. Azhdarchidae gen. et sp. indet. (MDM 349), cervical vertebra from the Mifune Group. **A, B:** dorsal; **C, D:** right lateral; **E, F:** ventral; **G, H:** posterior views. Natural size. Abbreviations: nc, neural canal; ns, neural spine; pf, lateral pneumatic foramen; poex, postexapophysis; poz, postzygapophysis; rid, lateral ridge.

Table 1. Measurements of Azhdarchidae gen. et sp. indet. (MDM 349), cervical vertebra from the Mifune Group (in mm).

| | |
|---------------------------------------|------|
| preserved length | 65 |
| width of postzygapophyses | 25.5 |
| width of the centrum (preserved) | 15.5 |
| width of the centrum (reconstructed) | ≈ 13 |
| height of middle part (preserved) | 7 |
| height of middle part (reconstructed) | ≈ 11 |

synapomorphy (Kellner and Langston, 1996). Because the cervical vertebrae of *Z. linhaiensis* were not sufficiently described and illustrated without any detail (Cai and Wei, 1994), a detailed comparison with Japanese specimen cannot be made. Therefore, some of the variations described above could be related to the position of the cervical vertebrae in the neck (e.g. lateral margins, directions of the postzygapophyses).

The Azhdarchidae have been known to occur from the Cenomanian deposits of Morocco (Kellner and Mader, 1996); Turonian-Coniacian strata of Uzbekistan (Nessov, 1984); the Campanian Judith River Formation of Alberta, Canada (Currie and Russell, 1982); Campanian Two Medicine Formation of Montana, USA (Padian, 1984; Padian and Smith, 1992; Padian *et al.*, 1995); Campanian-Maastrichtian deposits of Senegal (Monteillet *et al.*, 1982); the Maastrichtian Javelina Formation of Texas, USA (Lawson, 1975; Kellner and Langston, 1996); Maastrichtian deposits in Jordan (Arambourg, 1959); and in late Maastrichtian deposits of Mèrignon, France (Buffetaut *et al.*, 1997). Along with the Chinese specimens mentioned above (*Z. linhaiensis*, late Cretaceous), the occurrence of Azhdarchidae in Japan extends the distribution of those pterosaurs during the Cretaceous to the easternmost part of Asia.

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The suprageneric classification of the foraminiferal genus *Murrayinella* and a new species from Japan

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Abstract. Japanese species of the foraminiferal genus *Murrayinella* have a roataliid aperture that is defined by a foraminal plate and umbilical coverplate. Our observations suggest that this genus must be transferred from the family Glabratellidae to the family Rotaliidae. Its morphological similarity to the genus *Schackoinella*, as shown by the presence of a peripheral spine on each chamber, must be a result of homeomorphic convergence. *Murrayinella* never possesses apertural grooves like those of glabratellids. We give a detailed description of the apertural structure of the Japanese species of *Murrayinella* and formally describe a new species, *M. bellula*.

Key words: benthic foraminifera, *Murrayinella*, Rotaliidae, suprageneric taxonomy.

Introduction

Species of the foraminiferal genus *Murrayinella* are common in shallow-water sediments of both the Sea of Japan and the Pacific Ocean. The following are well known species: *Murrayinella minuta* (Takayanagi, 1955), *Murrayinella globosa* (Millett, 1903), and *Murrayinella takayanagii* (Matoba, 1967), all of which have been reported from the late Pleistocene to Recent. Among them, *Murrayinella minuta* is the most common species in Japan. A *Murrayinella* species has also been reported from the early middle Miocene of Southwest Honshu, Japan (Nomura, 1990). The earliest appearance of the genus is thus not from the Pliocene (Loeblich and Tappan, 1987), but from the middle Miocene.

Despite its common occurrence, the systematic position of this genus is still confused. Heron-Allen and Earland (1915) originally described *Murrayinella murrayi* as a *Rotalia* species, while the allied form *M. globosa* was described as a *Discorbina* species by Millett (1903). Subsequently, other species now allocated to *Murrayinella* were placed in the genus *Pararotalia*, except for some other generic allocations such as “*Eponides*” (Ujiié, 1963) and *Praeglobotruncana* (McCulloch, 1977). Thus, many workers regarded *Murrayinella* as closely related to the Rotaliidae. However, Loeblich and Tappan (1987) placed *Murrayinella* in the Glabratellidae, referring to their earlier systematic review (Loeblich and Tappan, 1964), on the basis of Heron-Allen and Earland’s observation that suggested a different mode of reproduction from the Rotaliidae, and an apparent

similarity to the genus *Schackoinella* from the late Miocene of Austria (Weinhandl, 1958). Indeed, Haman and Christensen (1971) regarded *Murrayinella* as a synonym of *Schackoinella*.

Previous investigations lacked detailed comparative observations on the foraminal structure of these small taxa that were beyond the resolution power of binocular microscopes. We carried out detailed anatomical observations of the inner test by scanning electron microscope, using a method of Nomura (1983). As a result, all the species of this genus are shown to be devoid of radiating apertural grooves as in the glabratellids, instead their apertures have the foraminal plate and umbilical coverplate typical of the roataliids. We now describe the Japanese species, including a new species, in detail and discuss the suprageneric position of the genus *Murrayinella*.

Foraminal structures of *Murrayinella*

In general, the apertural structures of the genus *Murrayinella* resemble those of *Ammonia* or *Pararotalia* species which have a foraminal plate and umbilical coverplate. These basic features of the roataliid aperture are well shown in several species from Eocene sediments of the Paris Basin (Hottinger *et al.*, 1991) and from the Red Sea (Hottinger *et al.*, 1993; Revets, 1993) and Japan (Nomura and Takayanagi, 2000). The final aperture of *Murrayinella* is an umbilical to extraumbilical slit usually covered with numerous small spines. The penultimate and antepenultimate foramina are a high arch or rounded openings with the

foraminal plate on the proximal side and with the umbilical coverplate closing up the umbilical side of the slit-shaped aperture.

The foraminal structure of *Murrayinella* species fundamentally resembles the *Pararotalia*-type rather than the *Ammonia*-type (Nomura and Takayanagi, 2000). *Murrayinella minuta* and *M. bellula* deviate little from the *Pararotalia*-type foramen. However, the foraminal plate of *M. globosa* is variable, ranging from the *Pararotalia*-type foramen to a form which is close to the *Ammonia* type. A quite different type is found in *M. takayanagii*. The *Ammonia*- or *Pararotalia*-type foramen can be distinguished by the position of the foraminal plate. The base of the foraminal plate in the *Ammonia*-type foramen is formed on the umbilical side of the previous whorl and thus the foramen is arch-shaped, while that of the *Pararotalia*-type foramen bends towards the inner side of the apertural opening, forming a lip-like structure in its lower side (or proximal side). Thus, the foraminal plate of the *Pararotalia*-type foramen is called a lower lip in order to distinguish from a toothplate of Hottinger *et al.* (1991). This difference of foraminal structure is significant for the discrimination of larger forms of rotaliid taxa when discussing their phylogenetic relationships. However, we regard this difference in *Murrayinella* as a less significant criterion for the suprageneric classification of this genus, because of the situation in *M. takayanagii*. The foramen of *M. takayanagii* is exceptional for rotaliid taxa, because the foraminal plate and chamber flap are poorly developed in contrast to the well developed umbilical coverplate observed from the outside of the test. We consider that this aperture has no systematic significance for the phylogenetic reconstruction of the rotaliid taxa. We would retain all these kinds of foramina in the genus *Murrayinella*.

Discussion

The most recent suprageneric classification of the genus *Murrayinella* places it within the family Glabratellidae, superfamily Discorbacea, although knowledge of both its external and internal structures is imperfect (Loeblich and Tappan, 1987). Fariás (1977) proposed that *Murrayinella* should include *M. murrayi* and *M. globosa* (= *Rotalia erinacea* Heron-Allen and Earland), but the latter species has been regarded by some authors to be better placed in *Schackoinella* (Quilty, 1975). According to our observations, *Murrayinella* never shows the umbilical features, such as radial grooves, that aid attachment during plastogamy, the type of reproduction found in the Glabratellidae. The aperture of the Glabratellidae is a low interiomarginal slit on the umbilicus without additional internal structures. The observation reported by Heron-Allen and Earland (1915) for *M. murrayi* showing "double (budded) specimens" must be questioned. The aperture of *M. murrayi* and *M. globosa* is an umbilical to extraumbilical slit, which must make plastogamic reproduction impossible. We believe that Heron-Allen and Earland's budded specimens do not belong to *Murrayinella*. The external morphology of *Schackoinella* is similar to *Murrayinella*, but its aperture is mostly umbilical and has radial striations, typical of the Glabratellidae. These features clearly show that *Murrayinella* and

Schackoinella have a different phylogenetic origin. The most obvious way to distinguish *Murrayinella* and *Schackoinella* is provided by the internal structure of the aperture. The foraminal plate and the umbilical coverplate in *Murrayinella* are never found in *Schackoinella*.

Through our examination, we have found that the structure of the aperture in *Murrayinella* resembles that found in the Rotaliidae and the foraminal structure is similar to the *Pararotalia*-type foramen. Exceptionally, there is the intermediate form between the *Ammonia* type and the *Pararotalia* type and one more type of foramen that does not belong to either of them. In view of these varied foramina, it was difficult to decide whether this genus should be placed in the subfamily Pararotaliinae or subfamily Ammoniinae in the scheme of Loeblich and Tappan's (1987) suprageneric classification. Loeblich and Tappan (1987) defined the foramen of the subfamily Pararotaliinae as having a "single interiomarginal slitlike aperture, converted into areal intercameral foramen" that is the typical *Pararotalia*-type foramen. They did not refer to the foraminal structure in the subfamily Ammoniinae, but instead to structures associated with the aperture such as radial canals, fissures, and umbilical cavities. However, these structures are not restricted to the Ammoniinae. Members of the Pararotaliinae also have these structures (Hottinger *et al.*, 1991, 1993; Nomura and Takayanagi, 2000). A strict usage of these structures would not help to discriminate between the Ammoniinae and the Pararotaliinae. Instead, the distinction between the *Pararotalia*-type and the *Ammonia*-type foramen provides the best character for deciding on the subfamily placement (Nomura and Takayanagi, 2000). A supplementary structure, the labial aperture, is sometimes found in the *Ammonia*-type foramen but is never associated with the *Pararotalia* one. The foraminal structures of *Murrayinella* are rather simple and lack labial apertures. We are of the opinion that the difference between the Ammoniinae and the Pararotaliinae can be found in the foraminal structure and that this feature is most helpful for the subfamily-level classification. Therefore, we suggest that the placement of this genus in the subfamily Pararotaliinae and in the family Rotaliidae is valid.

Systematic descriptions

Order Rotaliida Lankester, 1885
Superfamily Rotaliacea Ehrenberg, 1839
Family Rotaliidae Ehrenberg, 1839
Subfamily Pararotaliinae Reiss, 1963
Genus *Murrayinella* Fariás, 1977

Type species.—*Rotalia murrayi* Heron-Allen and Earland, 1915.

Emended description.—Test small, low trochospiral to high trochospiral with depressed or opened umbilicus; inflated to globular chambers usually rough with numerous small spines, four to six in the final whorl; sutures depressed to deeply depressed; periphery rounded to angled, usually lobulate; aperture a low interiomarginal slit located extraumbilically; apertures in preceding chambers rounded; walls hyaline, rough and translucent.

Remarks.—Loeblich and Tappan (1987) placed this genus in the family Glabratellidae Loeblich and Tappan (1964), based on their interpretation of Heron-Allen and Earland's claim to have observed double (or budded) specimens in the type species. *Rotalia erinacea* Heron-Allen and Earland and *Discorbina imperatoria* var. *globosa* Millett were placed in the genus *Schackoinella* Weinhandl by Quilty (1975), which also belongs to the family Glabratellidae.

These observations strongly influenced Loeblich and Tappan's (1987) decision to place this genus in the glabratellids. However, Whittaker and Hodgkinson (1979) once considered *Murrayinella* to be conspecific with *Schackoinella*, but they immediately changed their opinion after examining Quilty's description of the type species *Schackoinella sarmatica* Weinhandl. In the postscript of their monographic paper, they suggested that the difference

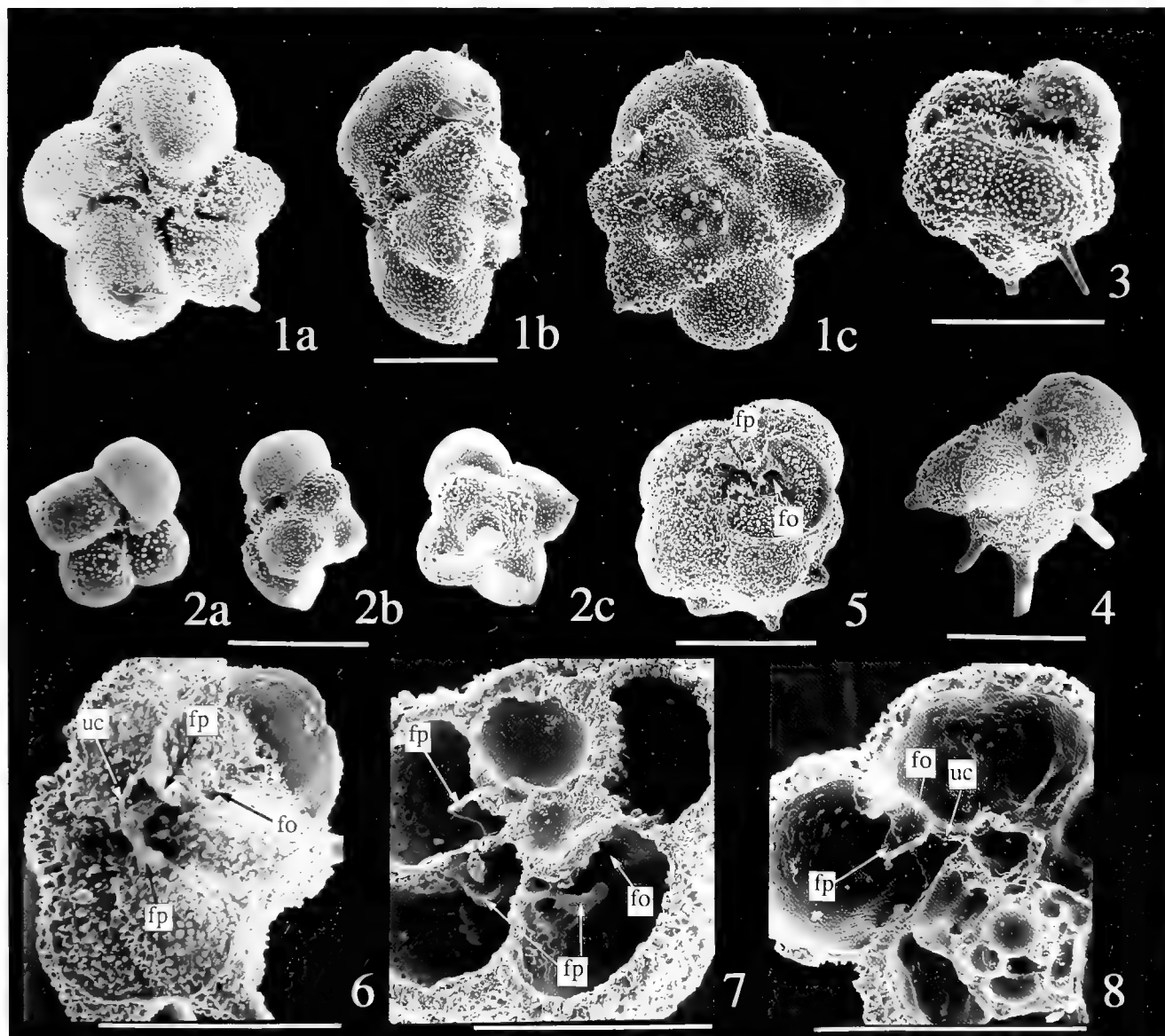


Figure 1. *Murrayinella globosa* (Millett) from Holocene bay-floor muds of Tateyama, Chiba Prefecture. Scale bar: 100 μ m. **1a–c.** Mature specimen. **2a–c.** Immature specimen. **3.** Obliquely viewed specimen showing the marginal slit of the aperture. **4.** Peripheral view of specimen without the final chamber showing the arched opening of the penultimate foramen. **5.** Oblique view of specimen without the final chamber showing the foraminal plate. **6.** Oblique view of the penultimate and antepenultimate foraminal plates (fp) and the penultimate umbilical coverplate (uc). fo = foramen. **7.** Specimen with dorsal chambers removed showing the foraminal plate (fp) protruded from each foramen (fo). **8.** Specimen with ventral chambers removed showing the foraminal plate (fp) from the penultimate foramen (fo) and the umbilical coverplate (uc).

in the aperture and the ventral feature formed a basis for discriminating between *Murrayinella* and *Schackoinella*. As observed herein, the basic structure of the *Murrayinella* aperture is the same as that of the rotaliids. Both are characterized by the foraminal plate and umbilical coverplate. The final aperture of *Murrayinella* is always an umbilical to extraumbilical slit, but the previous foramina are rounded to oval openings as a result of the umbilical side-slit being partly closed up by the umbilical coverplate. This apertural structure can only be explained by the rotaliid aperture and foraminal model (Hansen and Reiss, 1971; Nomura and Takayanagi, 2000).

Murrayinella globosa (Millett)

Figure 1.1–1.8

Discorbina imperatoria (d'Orbigny) var. *globosa* Millett, 1903, p. 701, pl. 7, figs. 6a–c.

Rotalia erinacea Heron-Allen and Earland, 1915, p. 720, pl. 53, figs. 23–26.

"*Eponides*" *globosa* (Millett). Ujiie, 1963, p. 233, pl. 1, figs. 27a–29 (part).

Pararotalia cf. *imperatoria globosa* (Millett). Chiji and Lopez, 1968, pl. 12, figs. 5a–c.

Pararotalia murrayi (Heron-Allen and Earland). Chiji and Lopez, 1968, pl. 12, figs. 6a, b.

Pararotalia minuta (Takayanagi). Matoba, 1967, p. 256, pl. 27, figs. 5a, b.

Pararotalia? *globosa* (Millett). Matoba, 1970, p. 57, pl. 6, figs. 8a–c.

Schackoinella sarmatica Weinhandl. Haman and Christensen, 1971, p. 44, text-figs. 1–3.

Schackoinella globosa (Millett). Quilty, 1975, p. 331; Loeblich and Tappan, 1994, p. 142, pl. 294, figs. 1–10.

Murrayinella erinacea (Heron-Allen and Earland). Farias, 1977, pl. 1, figs. 7–10.

Schackoinella (?) *dissensa* McCulloch, 1977, p. 317, pl. 169, figs. 5, 10a–c, 11a, b, 12a–c.

Ammonia globosa (Millett). Zheng *et al.*, 1978, p. 49, pl. 5, figs. 7a–11c.

"*Schackoinella*" *globosa* (Millett). Whittaker and Hodgkinson, 1979, p. 63, pl. 5, figs. 11, 12a, b, pl. 10, fig. 6 (transferred to the genus *Murrayinella* in postscript).

Pararotalia aff. *globosa* (Millett). Oki, 1989, p. 133, pl. 15, figs. 9a–d.

Murrayinella globosa (Millett). Matoba and Fukasawa, 1992, fig. 9, nos. 16a–c.

Examined specimens.—Specimens from Holocene bay-floor muds (7400–4100BP) of Tateyama, southern part of the Boso Peninsula. Sample locality is given by Fujiwara *et al.* (1997) as in the cliff of the Heguri-gawa River, approximately 139°52'55"E and 35°0'27"N.

Description.—Test rather small, planoconvex with a convex ventral side and flat to slightly inflated dorsal side; periphery lobulate and with a short transparent spine on each chamber; sutures distinct, radiate, deeply depressed on ventral side, and curved on dorsal side; chambers four to five on ventral side, inflated; aperture indistinct with a covering of small spines, but apparently an umbilical to extraumbilical slit; wall rough and hispid, usually transparent; pores present, but usually indistinct with small spines on walls, opti-

cally indistinctly radial.

Apertural structure.—The final aperture is an umbilical to extraumbilical slit and is covered with small spines (Figure 1.1–1.3). The foramen is arch-shaped (Figure 1.4, 1.5), with an umbilically extended foraminal plate and umbilical coverplate (Figure 1.6–1.8). The foraminal plate obliquely protrudes from the apertural face and its proximal part continues to the umbilical coverplate. The umbilical flap is distinct and adheres to the preceding ones. It has a narrow slit, but does not connect with the labial aperture.

Geographic occurrences.—Mostly limited to the Indo-Pacific region. In Japan, this species is widely distributed in the coastal areas of both the Sea of Japan and the Pacific.

Stratigraphic occurrences.—Known from the late Miocene (Whittaker and Hodgkinson, 1979) to the Recent.

Size and measurements.—Maximum test width is 250 μ m, maximum test length is 171 μ m; minimum test width is 99 μ m, minimum test length is 63 μ m; averaged test width is 166 μ m, averaged test length is 114 μ m.

Remarks.—Heron-Allen and Earland (1915) placed this species in *Rotalia*, and erroneously renamed it *Rotalia erinacea*, since they believed that the original name was pre-occupied by *Rotalia globosa* (Hantken) (see Whittaker and Hodgkinson, 1979 for further discussion). However, later workers suggested the placement in *Rotalia* was invalid, because of its rather different test morphology. This species is characterized by a small test and rough test surface totally covered with small spines, which obscure the details of the apertural structure. Ujiie (1963) considered it to belong to the genus *Eponides*, but he also questioned this generic placement, because of the different nature of the undeveloped inframarginal sulcus around the aperture, the wall lamellarity, and other subordinate external differences of test. Based on our detailed observation, however, the aperture of this species is an extraumbilical slit similar to the rotaliid one. The foraminal plate and the umbilical coverplate, which are basic components in the rotaliid aperture, are present but the foraminal plate is very variable. In general, these structures resemble the *Pararotalia*-type foramen. However, some specimens have the *Ammonia*-type foramen proposed by Nomura and Takayanagi (2000). Nevertheless, the base of the foraminal plate is not well developed in comparison with typical form of the *Ammonia*-type foramen that shows a hook-like structure. As far as the apertural structure is concerned, this species conforms to the *Pararotalia*-type foramen. Otherwise, it is usually characterized by a depressed umbilicus, where the chamber flaps are closely imbricated and fused to make a more rough umbilicus surface. Such features, and the covering of small spines, are enough to separate this species from both *Ammonia* and *Pararotalia* and to warrant a separate genus *Murrayinella*.

Murrayinella globosa has been confused with *M. murrayi* (Heron-Allen and Earland, 1915) by some workers. Hatta and Ujiie (1992) considered these two species to be conspecific, based on the opinion that there are gradational changes between the peripheral spines of *M. globosa* and the acute papillae of *M. murrayi*. However, *M. murrayi* has six chambers in the final whorl and a more convex umbilical side of the test (Heron-Allen and Earland, 1915) and surface

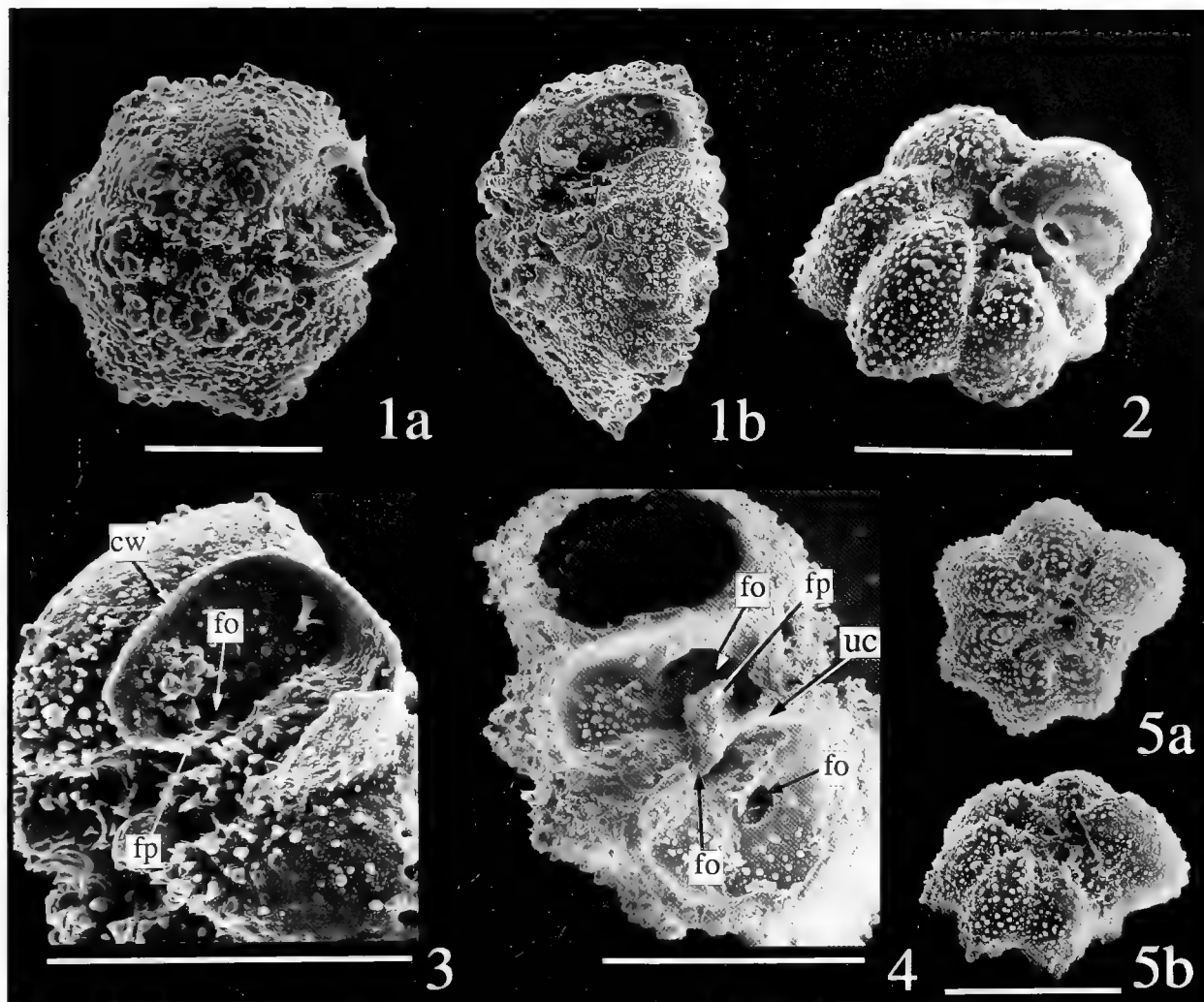


Figure 2. *Murrayinella minuta* (Takayanagi) from Holocene bay-floor muds of Tateyama, Chiba Prefecture. Scale bar: 100 μ m. **1a, b.** Mature specimen **2.** Obliquely viewed specimen showing the penultimate foramen with broken foraminiferal plate. **3.** Penultimate foramen with final chamber wall removed showing the basal part of the foraminiferal plate (fp) extended from the inside of the penultimate foramen (fo). cw = chamber wall. **4.** Obliquely sectioned specimen showing the preceding foramen with the foraminiferal plate (fp) and the umbilical coverplate (uc). fo = foramen. **5a, b.** Immature specimen.

rugosity (Whittaker and Hodgkinson, 1979), while *M. globosa* has four to five chambers in the final whorl and a depressed umbilical center without a distinct protrusion.

Murrayinella minuta (Takayanagi)

Figure 2.1–2.5

- Rotalia?* *minuta* Takayanagi, 1955, p. 45, 52, text-figs. 29a–c.
Pararotalia murrayi (Heron-Allen and Earland). Ujiie, 1963, p. 239, pl. 3, figs. 3a–9.
Pararotalia? *minuta* (Takayanagi). Matoba, 1970, p. 58, pl. 6, figs. 5a–c, 6a–c, 7a–c.
Praeglobotruncana (?) *wordeni* McCulloch, 1977, p. 424, pl. 178, figs. 7, 10, pl. 179, figs. 7, 8.

Pararotalia minuta (Takayanagi). Huang, 1980, p. 55, pl. 1, figs. 1–6, pl. 2, figs. 1–6, pl. 3, figs. 1–6, pl. 4, figs. 1–6.

Pararotalia globosa (Millet). Hatta and Ujiie, 1992, p. 198, pl. 43, figs. 5a–c.

Murrayinella minuta (Takayanagi). Matoba and Fukasawa, 1992, fig. 9, nos. 17a–c; Kamemaru, 1996, pl. 20, figs. 3, 4.

Examined specimens.—Specimens from Holocene bay-floor muds (7400–4100BP) of Tateyama, southern part of the Boso Peninsula. Sample locality is given by Fujiwara *et al.* (1997) as in the cliff of the Heguri-gawa River, approximately 139°52'55"E and 35°0'27"N.

Emended description.—Test small, planoconvex with a strongly convex ventral side and nearly flat dorsal side; su-

tures distinct, nearly straight, radiate, slightly depressed in mature specimens and depressed in immature specimens on ventral side, and oblique and curved on dorsal side; chambers five to six on ventral side, slightly inflated, but more inflated on ventral side in immature stage; umbilicus nearly closed and with protruded plug in mature, but slightly open in immature specimens; aperture indistinct with small covering spines, but appears to be an umbilical to extraumbilical slit; wall rough and hispid, usually translucent; pores present, but indistinct with small spines on the walls, optically indistinctly radial.

Apertural structure.—The final aperture is an umbilical to extraumbilical slit with a poorly developed umbilical flap (Figure 2.1–2.3, 2.5). The foramen is oval and oblique to the base of the apertural face, with an umbilically extended foraminal plate (Figure 2.4). The protruded foraminal plate is close to the umbilicus and much inclined to the apertural face. The base of the foraminal plate extends onto the distal side of the foramen, forming a lip-like structure (Figure 2.2). The umbilical coverplate is formed, but it does not cover the labial aperture in the preceding foramen.

Geographic occurrences.—This species is widely distributed in the coastal areas of both the Sea of Japan and the Pacific. Huang (1980) reported it from the Taiwan Strait at depths ranging from 5.5 to 100 m.

Stratigraphic occurrences.—Known from the Late Quaternary to the Recent.

Size and measurements.—Maximum test width is 218 μm , maximum test length is 193 μm ; minimum test width is 133 μm , minimum test length is 81 μm ; averaged test width is 177 μm , averaged test length is 124 μm .

Remarks.—*Murrayinella minuta* (Takayanagi) was originally tentatively placed in the genus *Rotalia* because it had a closed umbilicus different from that of *Rotalia* as well as hispid walls. Later Ujiie (1963) considered this species to be synonymous with *Rotalia murrayi* and placed it in *Pararotalia* on account of the apertural and foraminal structures. However, Matoba (1970) separated it from *murrayi*, stating that *minuta* has a strongly convex ventral side and flat dorsal side, while *murrayi* has a subglobular test with convex dorsal side and rounded periphery. We support his suggestion that *minuta* is different from *murrayi*.

The variable form of this species is similar to *M. globosa* in having a more lobulate periphery and the incipient spines in earlier chambers of the last whorl. McCulloch (1977) regarded one such variant as a new species that she tentatively assigned to the genus *Praeglobotruncana*. However, these characters fall within the range of *minuta*'s variation.

Ujiie (1963) was the first to discuss the apertural structure of this species and mentioned that it has a toothplate (= the foraminal plate and umbilical coverplate) connected with the preceding foramen. His observation follows the result of Loeblich and Tappan (1957) who studied the type species of the genus *Pararotalia* [i.e., *P. inermis* (Terquem)]. Thus, he put this species in the genus *Pararotalia*. On the basis of observations of the internal structure of *P. inermis* given by Reiss and Merling (1958), he further mentioned that the anterior side of the foraminal plate of *M. minuta* is abruptly cut off at a distance of half a chamber length. Ujiie's observations are important for understanding the true nature of this

apertural structure. The foraminal plate of the *Pararotalia*-type foramen looks like a lip in the lower side of the foramen, resulting from the inward extension of the basal part of the foraminal plate to the distal side of the aperture (Nomura and Takayanagi, 2000). We agree that the aperture and foramen of *minuta* are therefore the same as in *Pararotalia*. The foraminal structure seen by us was also noted by Huang (1980) who showed the foraminal plate (his lip) associated with the one side of the foramen (e.g., Huang, 1980, pl. 2, figs. 2–4). This feature suggests the close phylogenetic relation of *minuta* to *Pararotalia* species. Except for the apertural similarity, however, the small test and the rough test surface are diagnostic enough to separate *minuta* from *Pararotalia* and keep it in *Murrayinella*.

Murrayinella takayanagii (Matoba)

Figure 3.1–3.3

Pararotalia minuta (Takayanagi) var.. Matoba, 1967, p. 256, pl. 27, figs. 6a, b.

Pararotalia ? *takayanagii* Matoba, 1970, p. 63, pl. 6, figs. 9a–c, 10 a–c.

Murrayinella takayanagii (Matoba). Takayanagi and Hasegawa, 1986, pl. 2, figs. 3a–c.

Examined specimens.—Four specimens from the Pleistocene of Well Kashimaoki SK-1, donated by Prof. S. Hasegawa, Hokkaido University; three specimens from the Recent sediment of Matsushima Bay (paratypes), donated by Prof. Y. Matoba, Akita University.

Emended description.—Test very small, low trochospiral, planoconvex to concave-convex; spiral side of test gently concave due to the inflation of chambers of the last whorl; periphery subrounded and strongly lobulate becoming stellate; umbilical side deeply concave, usually open without a plug; chambers five to five and one half in final whorl, inflated on periphery; sutures depressed on both umbilical and spiral sides; wall calcareous, thin, very finely perforate, covered with small pustules, peripheral area in each last whorl chamber with blunt spines; aperture arch-shaped and large for test, opened to umbilicus with narrow overturned lip.

Apertural structure.—The foraminal plate is poorly developed, but each umbilical coverplate is clearly shown around the umbilicus (Figure 3.1–3.3). The umbilical coverplate is inflated toward the umbilicus, thus it looks like a part of the chamber wall.

Geographic occurrences.—This species is known in the northern Pacific coast of Honshu Island, Japan.

Stratigraphic occurrences.—Known from the Pleistocene to the Recent.

Size and measurements.—Maximum test width is 135 μm , maximum test length is 69 μm ; minimum test width is 119 μm , minimum test length is 53 μm ; averaged test width is 127 μm , averaged test length is 59 μm .

Remarks.—The well developed final aperture, and the widely opened and depressed umbilicus are characteristics of this species. Matoba (1970) placed it in the genus *Pararotalia*, based on the similarity of the aperture to that of *Pararotalia minuta*. However, the systematic position of this species has been questioned, because it lacks the umbilical

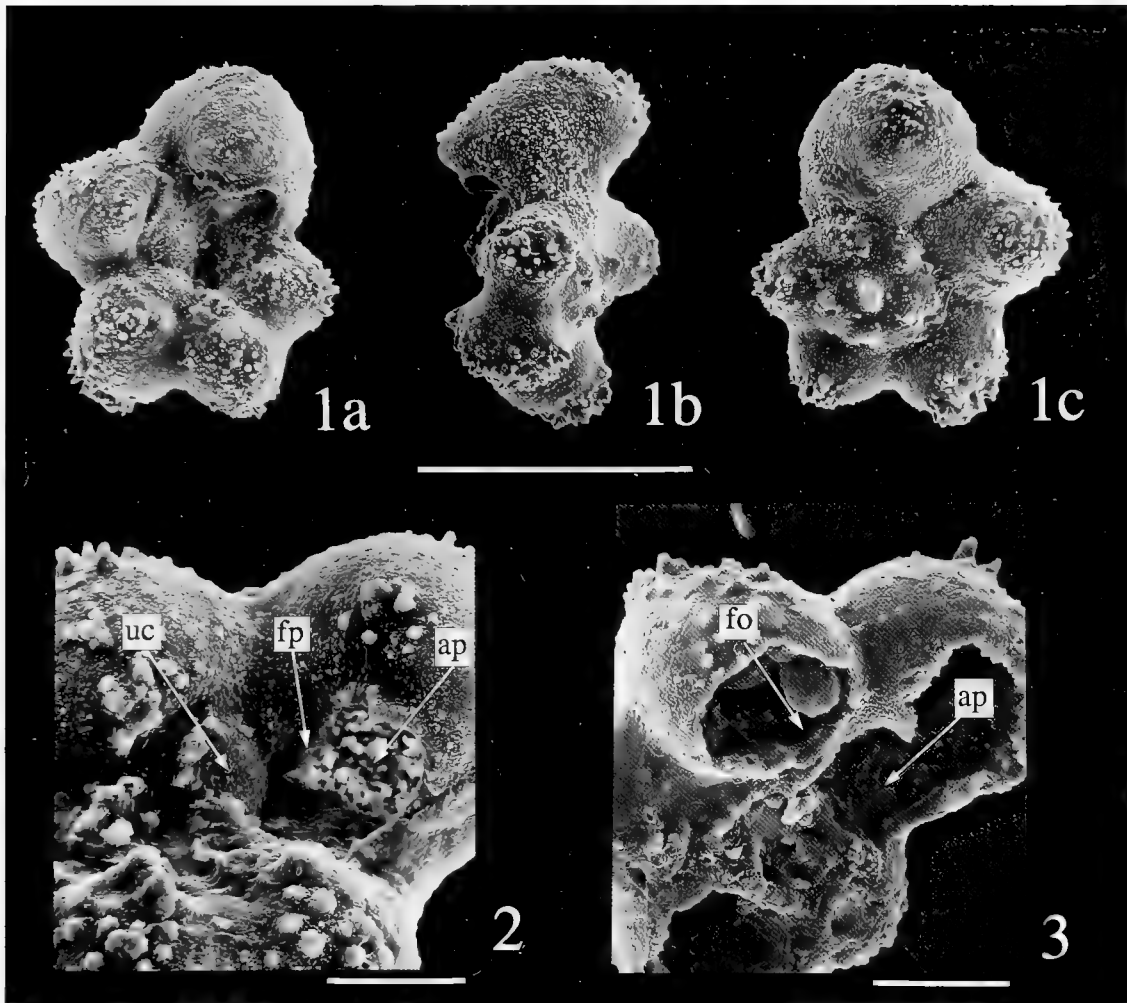


Figure 3. *Murrayinella takayanagii* (Matoba) from the Pleistocene of Well Kashimaoki SK-1. **1a–c.** Mature specimen. Scale bar: 100 μ m. **2.** Enlargement of aperture (ap) showing the small foraminal plate (fp) and a completely covered umbilical coverplate (uc). Scale bar: 20 μ m. **3.** Umbilical section of no. 2 specimen showing the internal rim of the penultimate foramen (fo). ap = aperture. Scale bar: 30 μ m.

plug that is a characteristic feature of *Pararotalia*. After examining these systematic problems, we are of the opinion that the aperture of *takayanagii* is fundamentally comparable to the foraminal plate and umbilical coverplate concept of the rotaliids, but these features at the same time are somewhat different from their expression in *Pararotalia*. The aperture of *takayanagii* is usually rounded, without special developments such as the umbilical flap, while that of *Pararotalia* is an extraumbilical slit with a development of both the foraminal plate (=lower lip of Nomura and Takayanagi, 2000) and an umbilical coverplate. Because the chamber flap is poorly developed in *takayanagii*, the umbilical coverplate that partly conceals the umbilical side of the foramen is clearly shown in the umbilical view. The foraminal plate itself is less developed and is not clearly differentiated from the chamber wall. These apertural characters, and the ab-

sence of the umbilical plug, both strongly suggest that the placement of this species in *Pararotalia* is inappropriate.

On the basis of the basically trochospiral nature of the test, and taking the hispid nature of the test surface and the basic apertural structure of this species into consideration, we have put *takayanagii* in the genus *Murrayinella*.

Murrayinella bellula sp. nov.

Figures 4.1–4.2; 5.1–5.6; 6

"Eponides" globosa (Millett). Ujiie, 1963, p. 233, pl. 1, fig. 26 (part).

Diagnoses.—Highly trochospiral test with inflated globular chambers; walls hispid; one spine usually in the earliest portion of the test; aperture an umbilical slit; foramen associated with a lip-like foraminal plate and an umbilical coverplate.

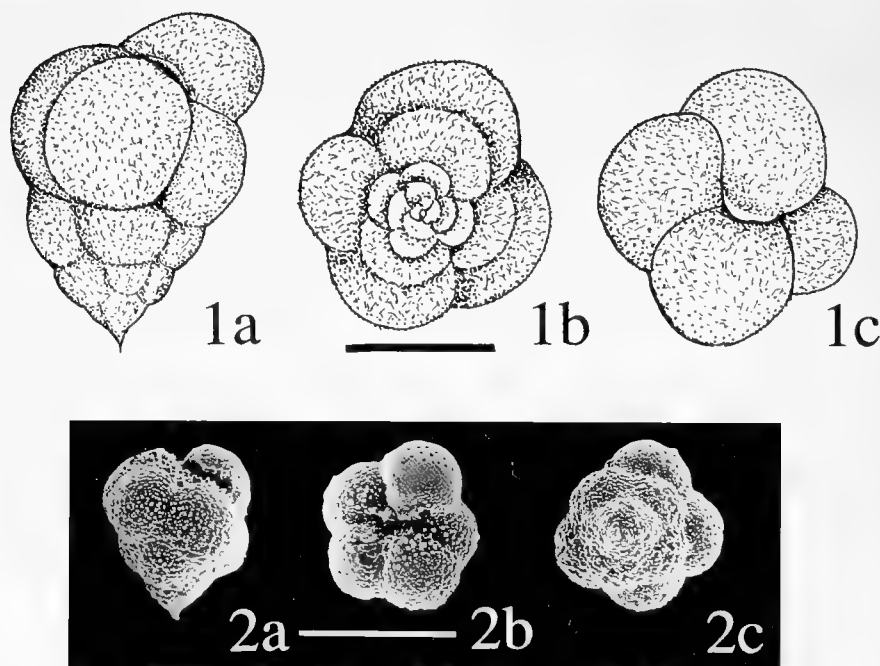


Figure 4. 1a–c. Holotype (NFL 9901) of *Murrayinella bellula* sp. nov. from Holocene bay-floor muds of Tateyama, Chiba Prefecture. 2a–c. Paratype (NFL 9902) of *Murrayinella bellula* sp. nov. Scale bar: 100 μ m.

Holotype and paratypes.—Holotype (registered number, NFL 9901), Figure 4. 1a–c, Holocene bay-floor muds (7400–4100BP) in Tateyama, Chiba Prefecture; paratypes (registered number, NFL 9902), Figure 4. 2a–c, from the same deposits. Sample locality is given as number 7 by Fujiwara *et al.* (1997) in the cliff of the Heguri-gawa River, approximately 139°52'55"E and 35°0'27"N.

Depository.—Holotype, paratypes and figured specimens are deposited in Nomura Foraminiferal Laboratory, Shimane University (NFL).

Description.—Test small, cone-shaped, with a strongly convex ventral side and nearly flat dorsal side; sutures distinct, radiate, and depressed on ventral side; chambers four to five on ventral side, inflated; periphery lobulate in final whorl; aperture indistinct and covered with small spines, but an umbilical slit; wall rough and covered with very small pustules; pores present, but indistinct due to rough surface, optically indistinctly radial.

Apertural structures.—The final aperture is an umbilical slit and is covered with small spines (Figure 5.3). The foramen is elongate, oval and obliquely arranged to the plane of the whorl (Figure 5.2). The foraminal plate is formed at the base of the foramen and protruding from it (Figure 5.1, 5.4–5.6). The umbilical coverplate is continued from the foraminal plate and conceals the umbilical side of the foramen (Figure 5.4, 5.5).

Geographic occurrence.—This species is common in the Holocene bay-floor muds (tsunami deposits) in Tateyama, southern part of the Boso Peninsula. Ujiie (1963) recorded

this species from Tokyo. Thus, the known geographic distribution is limited to the Kuwanto area.

Stratigraphic occurrences.—Known only from the Holocene.

Size and measurements.—Maximum test width is 215 μ m and maximum test length is 196 μ m; minimum test width is 97 μ m and minimum test length is 80 μ m; averaged test width is 139 μ m and averaged test length is 129 μ m.

Remarks.—This new species is characterized by its high trochospiral coil and rough test surface. The foraminal structure is of the rotaliid type consisting of foraminal plate and umbilical coverplate. The foraminal plate is much inclined to the previous whorl and forms a prominent plate in the lower side of the foramen, whose structure is the same as the *Pararotalia*-type foramen described by Nomura and Takayanagi (2000).

The umbilical view of this species is similar to that of *M. globosa* in having four to five globular chambers in the final whorl and suggests a close phylogenetic relationship with the latter. Ujiie (1963) regarded this form as a variant of *M. globosa*. However, the size distribution (test length and maximum width) indicates the isolated position of this new species from *M. globosa*, particularly for mature individuals (Figure 6). A discriminant analysis also indicates statistically significant differences between the two species. Moreover, this species possesses a short spine in the initial chamber, but is usually devoid of spines in subsequent chambers. This spine is one of the characteristics of the new species.

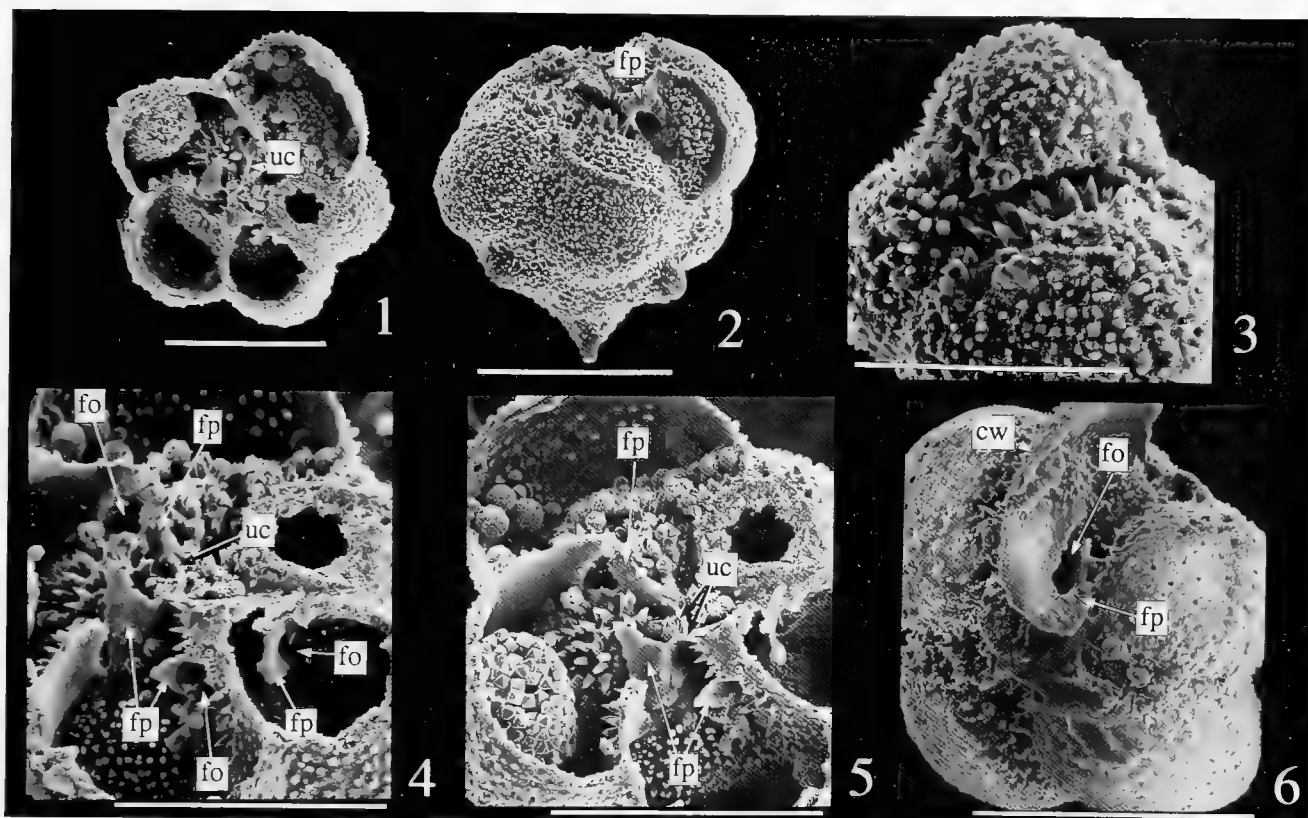
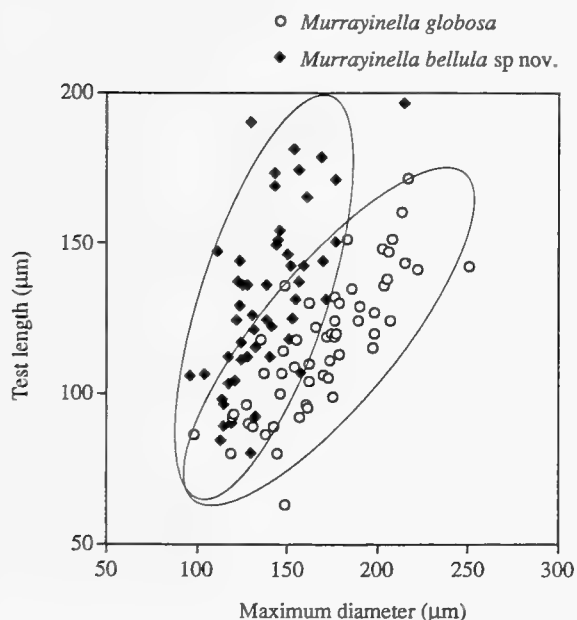


Figure 5. Details of *Murrayinella bellula* sp. nov. Scale bar: 100 µm. 1. Sectioned specimen with ventral chambers removed. uc = umbilical coverplate. 2. Oblique view of specimen showing the small spines and foraminiferal plate (fp) with oval opening of penultimate foramen. 3. Mature specimen showing the slit aperture with hispid crystals. 4. Closeup of no. 1 showing the protruded foraminiferal plates formed in the lower side of the foramen. fo = foramen, fp = foraminiferal plate, uc = umbilical coverplate. 5. Another view of no. 4. fp = foraminiferal plate, uc = umbilical coverplate. 6. Oblique view of penultimate foramen (fo) with foraminiferal plate (fp) and the remains of final chamber wall (cw).



Murrayinella bellula occurs in sand and sandy gravel beds in association with abundant *Ammonia japonica*, *Pseudononion japonicum* and miliolids, an assemblage apparently indicative of shallow marine conditions with some influence of brackish water. The assemblage containing this new species also includes planktic and some offshore species such as *Uvigerina proboscidea*, *Planocassidulina helenae*, *Bulimina marginata*, and *Brizalina striata*. These offshore-cum-brackish assemblages may derive from the Pleistocene Kazusa Group, which contains a well preserved offshore and shallow-water foraminiferal assemblage. However, Fujiwara *et al.* (1997) proposed that such a mixed occurrence of bay to offshore foraminiferal assemblages in the bay-floor muds could be explained by a tsunami event based on the analyses of the sedimentary facies and sequence. This species possibly came from the shallower

Figure 6. Size distribution of *Murrayinella globosa* (Millet) and *M. bellula* sp. nov. plotted against axes of maximum diameter and test length. Ellipsoids indicating a 95% confidence region for each species.

coastal environment.

Etymology.—The specific name is derived from Latin *bellulus*, pretty, referring to its small and delicate test.

Conclusions

We described four Japanese species of *Murrayinella*, including one new species, from the Late Quaternary tsunami deposits in Tateyama, in the southern part of the Boso Peninsula. Detailed observations of the *Murrayinella* aperture indicate that the grooves radiating from the aperture that are so diagnostic of the glabratellids are never developed. Instead, *Murrayinella* has a foramen associated with a foraminal plate and umbilical coverplate, which is typical of rotaliids. We therefore suggest that the suprageneric placement of *Murrayinella* is not in the family Glabratellidae, but the Rotaliidae.

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Upper premolar dentitions of *Deperetella birmanica* (Mammalia: Perissodactyla: Deperetellidae) from the Eocene Pondaung Formation, Myanmar

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Abstract. Discovery of upper premolar dentitions of *Deperetella birmanica* (Mammalia: Perissodactyla: Deperetellidae) from the Eocene Pondaung Formation, central Myanmar (= Burma) throws a new light on previously confused species- and genus-level systematics of *Deperetella* and its related genus *Diplophodon*. Clarification of the relationship among the *Deperetella* species is particularly important for correlation of Eocene mammal faunas in Asia. The newly discovered material show the characteristics of the previously unknown upper premolar dentition of *D. birmanica*, demonstrating that *Deperetella similis* (the type species of the genus *Diplophodon*) from China is a junior synonym of *Deperetella birmanica* and that *D. birmanica* is clearly distinguishable from all other species of *Deperetella*. The genus *Diplophodon*, to which *D. birmanica* has often been allocated, is regarded conventionally as a junior synonym of *Deperetella* because this genus is not sufficiently distinct from *Deperetella* to warrant generic separation. The presence of *D. birmanica* and its comparable species in several Eocene deposits of Myanmar, China and Mongolia suggests that these deposits are roughly contemporaneous.

Key words: *Deperetella*, Deperetellidae, *Diplophodon*, Eocene, Myanmar, Pondaung Formation

Introduction

Deperetella is an Asian Eocene tapiroid perissodactyl genus and was proposed by Matthew and Granger (1925a) based on *Deperetella cristata* Matthew and Granger, 1925a as the type species. This genus and *Teleolophus* Matthew and Granger, 1925b, which together constitute the family Deperetellidae Radinsky, 1965, are among the most common elements of the middle to late Eocene mammal fauna in Asia and important for correlation of Eocene mammal faunas in this area. Zdansky (1930) proposed *Diplophodon* and described *Diplophodon similis* as the type species. Of several species in the genus *Deperetella*, *Deperetella birmanica* (Pilgrim, 1925) from the Pondaung Formation, Myanmar has been sometimes referred to the genus

Diplophodon based on their small dental size and several of their dental characteristics (e.g. Ding *et al.*, 1977).

Previous classification of *Deperetella birmanica* and its related species has been much confused because these species were described on the basis of different parts of dentitions. *D. birmanica* was originally described by Pilgrim (1925) as *Chasmothereium? birmanicum* based on two mandibular rami of a single individual from the Eocene Pondaung Formation, central Myanmar. This was the only species of the Deperetellidae from the Pondaung Formation, and was questionably referred to the genus *Deperetella* by Colbert (1938). On the other hand, *Diplophodon similis* was described based on an upper dentition from the Heti Formation in the Yuanchu Basin of the Shanxi and Henan Provinces, China (Zdansky, 1930). Young (1937) reported

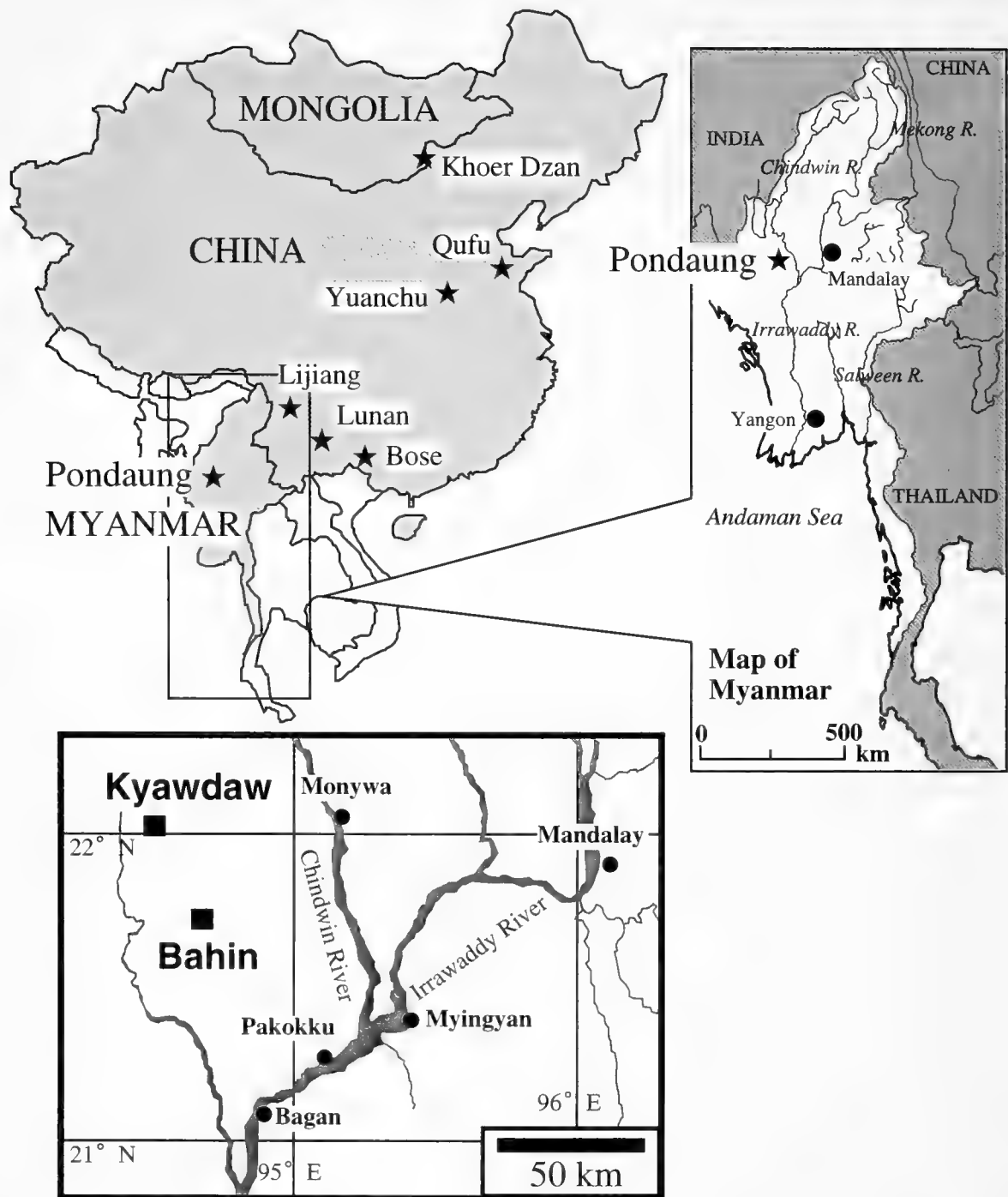


Figure 1. Maps showing distribution of several deperetellid-bearing deposits in Asia, names of place mentioned in this paper, and collecting sites of NMMP-KU 0005 and 0006. **Upper left map** showing locations of deposits that yielded *Deperetella birmanica* (Pilgrim, 1925) or *Deperetella* sp. cf. *D. birmanica* (black stars). Data from Colbert (1938), Li and Ting (1983), Russell and Zhai (1987), Shi (1989), Dashzeveg and Hooker (1997), and Huang (1999). **Upper right map** is topographic map of Pondaung area in central Myanmar, showing some major cities (black circles). **Lower map** showing collecting sites (black squares) of NMMP-KU 0005 and 0006 in the Pondaung Formation.

an additional upper dentition of *D. similis* from the same formation. Radinsky (1965) referred both *Chasmothereium?* *birmanicum* and *Diplophodon similis* to the genus *Deperetella*, and established a new family Deperetellidae. He mentioned that *D. birmanica* was related to *D. similis*. Chow *et al.* (1974) first reported the lower and additional upper dentitions of *D. similis* from the Lumeiyi Formation in the Lunan Basin of Yunnan Province, China, distinguishing *D. similis* from *D. birmanica* on the basis of several morphological differences in the lower dentitions.

The upper dentition of *D. birmanica* was discovered in Pondaung Formation during paleontological field research by Myanmar researchers in 1997 (Pondaung Fossil Expedition Team, 1997). In this study, we describe two maxillary fragments with premolars of *D. birmanica*. This discovery provides new information on the relationship of *D. birmanica* and *D. similis*.

Geological setting

The Pondaung Formation (Pondaung Sandstones) distributed in the central part of Myanmar (Figure 1) can be divided into "Lower" and "Upper" members for convenience: the "Lower Member" is mainly composed of greenish sandstone and is about 1,500 m thick in the type section; and the "Upper Member" is dominated by variegated-colored mudstone, about 500 m thick in the type section, and yields many mammalian and other vertebrate fossils (13 genera belonging to three orders; see Pilgrim and Cotter, 1916; Colbert, 1938; Holroyd and Ciochon, 1995; Jaeger *et al.*, 1999), indicative of a freshwater lagoonal environment (Colbert, 1938; Aye Ko Aung, 1999; Aung Naing Soe, 1999; Figure 2). The present material was recovered from the middle part of the "Upper Member" of the Pondaung

Formation. The Pondaung Formation grades downward into the Tabyin Formation (Tabyin Clay), and the two formations partially interfinger (Figure 2; Stamp, 1922; Bender, 1983). The Pondaung Formation is overlain by the Yaw Formation (Yaw Shale) with a distinct lithological break (Figure 2; Stamp, 1922; Bender, 1983). The Pondaung Formation is considered to date from middle to late Eocene based on the microfossil dating of the Tabyin Formation and the Yaw Formation (Bender, 1983; Figure 2). On the basis of the mammal fauna, the "Upper Member" of the Pondaung Formation has been considered most likely to be Bartonian age (late middle Eocene) (e.g. Russell and Zhai, 1987; Holroyd and Ciochon, 1994, 1995).

Systematic paleontology

Family Deperetellidae Radinsky, 1965

Genus *Deperetella* Matthew and Granger, 1925a

Diplophodon Zdansky, 1930, p. 35.

Type species.—*Deperetella cristata* Matthew and Granger, 1925a.

Other species included.—*Deperetella birmanica* (Pilgrim, 1925); *Deperetella depereti* (Zdansky, 1930) Radinsky, 1965; *Deperetella diensis* Chow *et al.*, 1974; *Deperetella khaitchinulensis* Reshetov, 1979; *Deperetella sichuanensis* (Xu *et al.*, 1979) Tong and Lei, 1983.

Distribution and age.—Asia. Middle to late Eocene.

Diagnosis.—"Deperetellids with premolar series longer than molars and posterior premolars molariform. P²⁻⁴ protolophs and metalophs slightly convergent to parallel, and separated lingually. P₁ and especially P₂ lengthened into shearing blades; P₃₋₄ with complete hypolophids. Molars relatively shorter and wider than those of *Teleolophus*. Manus tridactyl" (Radinsky, 1965, p. 222).

Remarks.—The genus *Diplophodon* was proposed by Zdansky (1930) based on an upper dentition of *Diplophodon similis* from the Heti Formation in China. Radinsky (1965) regarded *Diplophodon* as a junior synonym of *Deperetella*, although he recognized some characteristics that distinguished *Diplophodon* from *Deperetella*. Ding *et al.* (1977), in contrast, viewed *Diplophodon* as a distinct genus, in which *Diplophodon major* Young, 1937 and *Diplophodon birmanicum* were included. We follow Radinsky's (1965) view, because it is difficult to judge based on such a scanty fossil record whether the above-mentioned differences are intra- or intergeneric variations.

Deperetella birmanica (Pilgrim, 1925)

Figures 3, 4C–D

Chasmothereium? *birmanicum* Pilgrim, 1925, p. 25, pl. 2, fig. 9.

Diplophodon similis Zdansky, 1930, p. 35, pl. 1, fig. 35; Young, 1937, p. 419, fig. 5; Zong *et al.*, 1996, p. 83, pl. 32, fig. 4; Huang, 1999, p. 129.

Diplophodon major Young, 1937, p. 421, fig. 6.

Deperetella? *birmanicum* (Pilgrim, 1925). Colbert, 1938, p. 348, fig. 40. [sic]

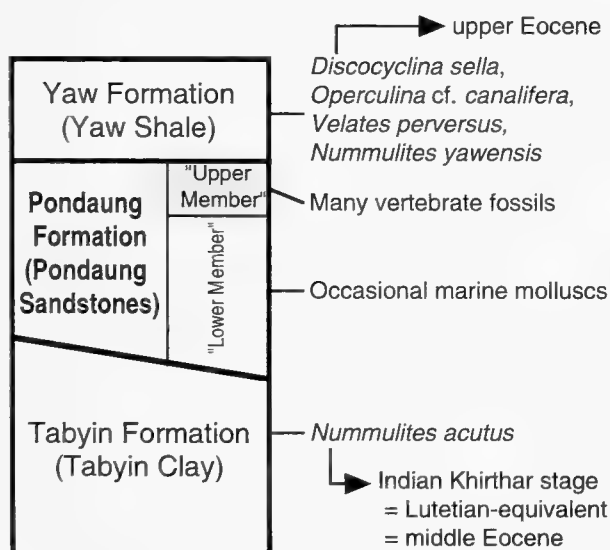


Figure 2. Generalized stratigraphy of middle to late Eocene deposits in central Myanmar and representative fossil species. Compiled from Stamp (1922), Eames (1951), Bender (1983), Holroyd and Ciochon (1994), and Aye Ko Aung (1999).

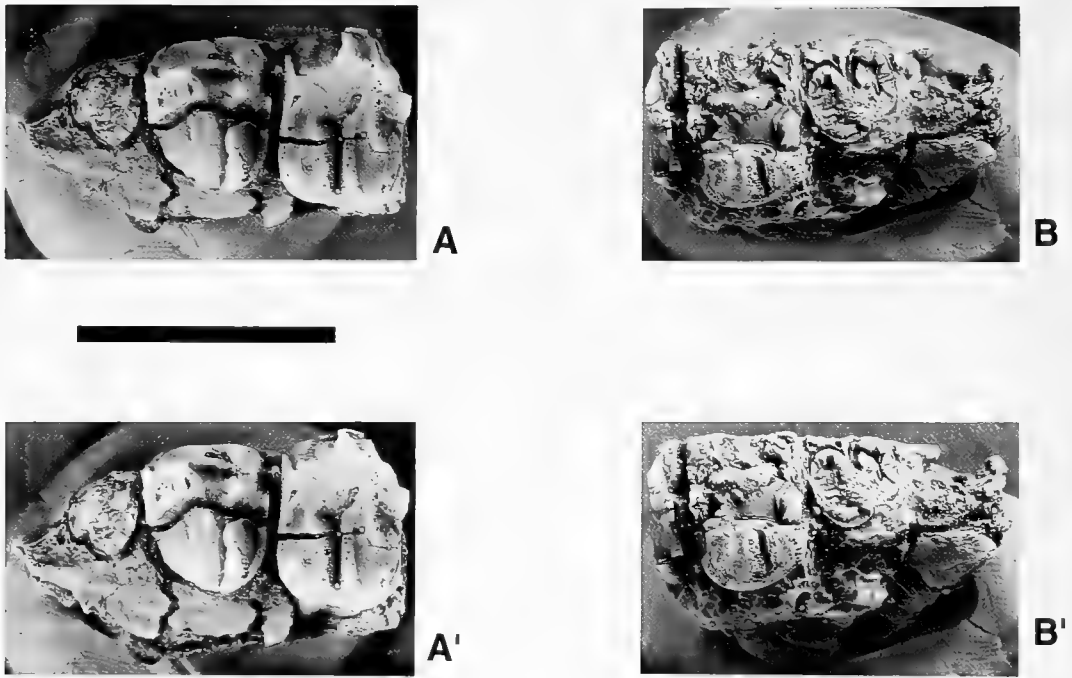


Figure 3. *Deperetella birmanica* (Pilgrim, 1925). **A, A'**. NMMP-KU 0005, stereo pair of fragmentary left upper jaw with broken P^{1-3} in occlusal view. **B, B'**. NMMP-KU 0006, stereo pair of fragmentary right upper jaw with broken P^{1-3} in occlusal view. Scale bar = 2 cm.

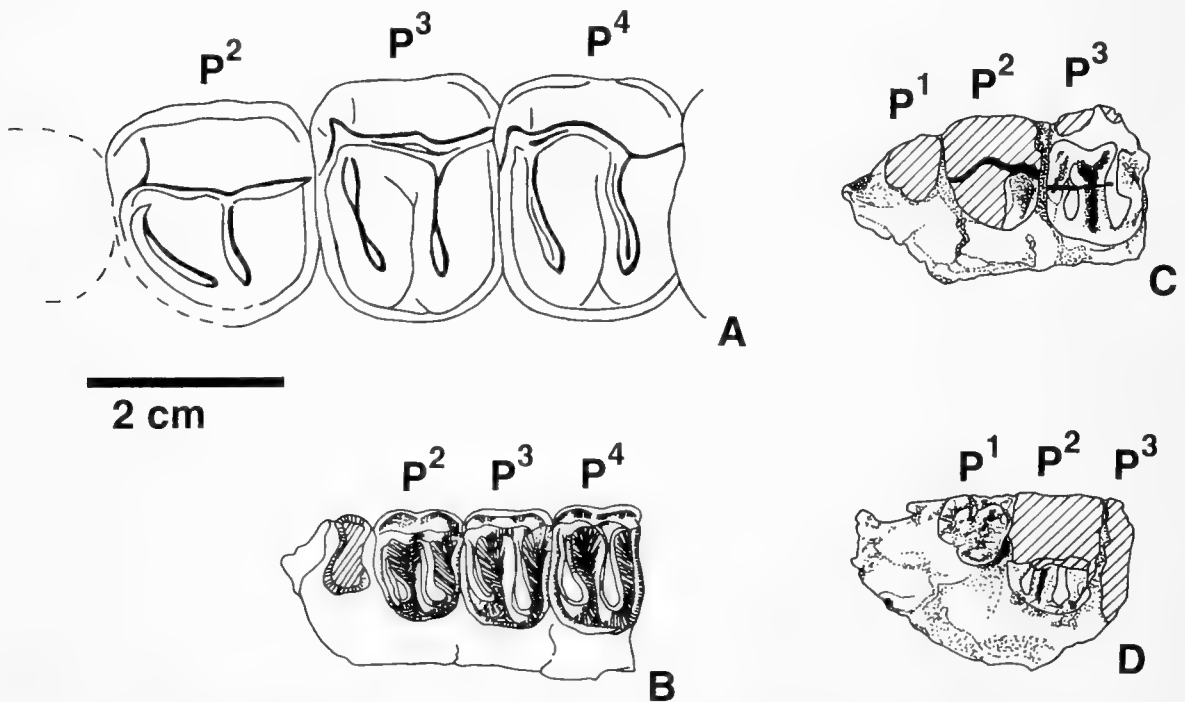


Figure 4. Upper premolar dentitions of *Deperetella cristata* Matthew and Granger, 1925a, "*Deperetella similis*" (Zdansky, 1930) and *Deperetella birmanica* (Pilgrim, 1925) in occlusal view. **A.** *D. cristata*, American Museum of Natural History (AMNH) No. 20290 with 20293, P^{2-4} , after Radinsky (1965, fig. 14). **B.** "*D. similis*" (Shanxi specimen), P^{2-4} , after Young (1937, fig. 5) and Radinsky (1965, p. 222, footnote 1). **C.** *D. birmanica*, NMMP-KU 0005, P^{1-3} . **D.** *D. birmanica*, NMMP-KU 0006, P^{1-3} (reversed). Scale bar = 2 cm.

Deperetella similis (Zdansky, 1930). Radinsky, 1965, p. 226; Chow *et al.*, 1974, p. 263, 272, pl. 1, fig. 3, 5–7.

Deperetella birmanicum (Pilgrim, 1925). Radinsky, 1965, p. 227. [sic]

Diplophodon cf. *similis* Zdansky. Ding *et al.*, 1977, p. 38, pl. 1, fig. 4.

Diplophodon birmanicum (Pilgrim, 1925). Ding *et al.*, 1977, p. 44, 45.

Diplophodon qufuensis Shi, 1989, p. 91, 99, pl. 1, fig. 7.

Material.—National Museum of the Union of Myanmar No. NMMP-KU 0005, a left maxillary fragment with roots of P¹, very heavily damaged P² and relatively complete P³; NMMP-KU 0006, a right maxillary fragment with roots of P¹, lingual one-third of P² and mesial margin of P³.

Locality.—NMMP-KU 0005 was from Bahin, Myaing Township, central Myanmar; NMMP-KU 0006 was from Kyawdaw, Palé Township, central Myanmar (Figure 1).

Horizon and age.—Middle part of the "Upper Member" of the Pondaung Formation (Figure 2), middle to late Eocene (most probably late middle Eocene).

Revised diagnosis.—A small-sized *Deperetella* with half the size of the type species *D. cristata*. The dental morphology is most derived in the genus. The molar cingulum is absent or weakly developed. P² is relatively shorter and wider than that of *D. cristata*. On P²⁻⁴, the proto-loph and metaloph are nearly parallel to each other, nearly perpendicular to the tooth row, and separated lingually.

Description.—P¹ has two buccolingually widened roots. The distal root is larger than the mesial one. Judging from

the roots, P¹ is longer than wide, and as long as and much narrower than P². No P¹ crown is preserved in the present material.

The crown of submolariform P² of each specimen is very poorly preserved. The proto-loph and metaloph appear to be nearly parallel to each other and nearly perpendicular to the tooth row. These two are separated lingually by a groove. The distal cingula are present. There seems to be no lingual cingulum, although the tooth of each specimen is heavily worn. The existence of mesial and buccal cingula, and the characteristics of buccal structures in the tooth are uncertain.

P³ is relatively better preserved in NMMP-KU 0005 than in NMMP-KU 0006, where only the broken anterior part of the tooth is preserved. P³ is more molariform and transversely larger than P². The proto-loph and metaloph are nearly parallel to each other, nearly perpendicular to the tooth row, and separated lingually by a groove. The mesial and distal cingula are present. There seems to be no lingual cingulum, although the tooth of each specimen is heavily worn. The buccal structures are not preserved. The proto-loph, paracone and metaloph form a slightly oblique, inverted U-shape, and the metacone is located as buccally as the paracone.

Dental measurements and comparison with other species are given in Table 1.

Discussion

NMMP-KU 0005 and 0006 possess submolariform premo-

Table 1. Measurements (in mm) of upper premolars of NMMP-KU 0005 and 0006 and some other species of *Deperetella*. Henan and Shanxi specimens are those described by Zdansky (1930) and Young (1937), respectively. Data for "*Deperetella similis*", *D. cristata* and *D. dienensis* are from Ding *et al.* (1977), Radinsky (1965) and Chow *et al.* (1974), respectively. Abbreviations: L, anteroposterior length; W, buccolingually width; AMNH, American Museum of Natural History; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology in Beijing, China.

| Specimen | P ¹ L | P ¹ W | P ² L | P ² W | P ³ L | P ³ W | P ⁴ L | P ⁴ W |
|---|---------------------|---------------------|---------------------|---------------------|---------------------|---------------------|---------------------|---------------------|
| <i>Deperetella birmanica</i> (Pilgrim) | | | | | | | | |
| NMMP-KU 0005 | 7.2 ¹ | 6.9 ¹ | 9.8 | 12.2 | 9.9 | 14.1 | | |
| NMMP-KU 0006 | 7.4 ¹ | 7.1 ¹ | 9.4 ² | | | | | |
| " <i>Deperetella similis</i> (Zdansky, 1930)" | | | | | | | | |
| Henan specimen (Zdansky, 1930) | | | | | 9.0 | 11.5 | 9.4 | 13.4 |
| Shanxi specimen (Young, 1937) | | | 9.0 | 10.8 | 9.0 | 12.3 | 9.5 | 13.0 |
| IVPP V29 | | | | | 10.0 | 12.8 | 10.7 | 14.3 |
| <i>Deperetella cristata</i> Matthew & Granger | | | | | | | | |
| AMNH 20290 | | | 19.9 | 21.8 | | | | |
| AMNH 20293 | | | | | 18.7 | 24.4 | | |
| <i>Deperetella dienensis</i> Chow <i>et al.</i> | | | | | | | | |
| IVPP V31.1 | | | | | | | 13.0 | 20.0 |

¹ The measurements are based on the roots, not on the crown.

² Estimated value.

lars (P^{2-3}) which are much wider than long and have a U-shaped crista that consists of a protoloph, paracone and metaloph. The protoloph and metaloph are arranged nearly parallel and lingually separated (Figures 3 and 4C–D). These characteristics of NMMP-KU 0005 and 0006 agree well with those of the upper premolar series of *Deperetella* diagnosed by Radinsky (1965). In *Deperetella*, the lower dentitions bear a diastema anterior to P_1 (Matthew and Granger, 1925a, fig. 5; Radinsky, 1965, fig. 14). Based on this fact, the presence of a diastema anterior to P^1 in its upper dentitions can be expected, though P^1 and anterior part to P^1 have not yet been discovered in any species of the genus. The presence of a diastema anterior to the most anterior tooth or tooth roots of both NMMP-KU 0005 and 0006 strongly suggests that these tooth or tooth roots are identifiable as P^1 .

NMMP-KU 0005 and 0006 are referred to the nominal species *Deperetella similis* from China, based on the similar size and dental morphology of the protoloph and metaloph that are nearly parallel to each other and nearly perpendicular to the tooth row on P^2 (Figure 4B–D and Table 1). *Deperetella cristata* has upper premolar dentitions much larger than the present specimens, and its protoloph and metaloph on P^2 are not parallel (Figure 4A). *Deperetella khaitchinulensis* and *Deperetella depereti* are similar to *D. cristata* in dental morphology (Dashzeveg and Hooker, 1997). The dental size of *D. khaitchinulensis* and *D. depereti* is larger than that of the present specimens. *Deperetella dienensis* is also similar to *D. cristata* in terms of dental morphology (Chow *et al.*, 1974), and its dental size is intermediate between those of *D. cristata* and the present specimens. *Deperetella sichuanensis* is similar in dental size to the present specimens, but the dental morphology of the former is the most primitive among the genus (Tong and Lei, 1984).

The only deperetellid previously recorded from the Pondaung Formation is *D. birmanica*, which has so far been represented only by lower dentitions. Radinsky (1965) noticed that *D. birmanica* is more closely related to *D. similis* than to other species of *Deperetella* based on the followings; the dentitions in *D. birmanica* and *D. similis* are nearly the same size, and lack the molar cingula, which are present in *D. cristata* and *D. depereti*. He did not synonymize *D. similis* to *D. birmanica*, because *D. birmanica* was represented only by a lower dentition, while *D. similis* was represented only by upper dentitions at that time. Ding *et al.* (1977) and Dashzeveg and Hooker (1997) also recognized the dental similarity between *D. similis* and *D. birmanica*. Chow *et al.* (1974) clearly distinguished *D. similis* from *D. birmanica* because *D. similis* lacks the posterior spur on P_4 and has broadly and posteriorly convex lophids on M_{1-3} in the lower dentition. However, these differences indicated by Chow *et al.* (1974) are not useful characteristics for separating the two species, since such are probably caused only by dental abrasion: the lower dentition in *D. birmanica* (Geological Survey of India (GSI) C348) is heavily worn, while the lower dentitions in *D. similis* (IVPP V713, V31) are almost intact (see Chow *et al.*, 1974, pl. 1, figs. 3, 5–7). *Diplophodon major* Young, 1937 from the Heti Formation in China was synonymized to *Deperetella similis* by

Radinsky (1965), and *Diplophodon qufuensis* Shi, 1989 from the Huangzhuang Formation in China was synonymized to *Diplophodon similis* (= *Deperetella similis*) by Zong *et al.* (1996) and Huang (1999). Zong *et al.* (1996) and Huang (1999) did not discuss the relationship between *D. birmanica* and *D. similis*, despite the fact that the two species are very similar. Our discovery of the upper premolar dentitions of this form strongly suggests that *D. similis* and *D. birmanica* are conspecific.

Deperetella birmanica is distinguished from the other species of *Deperetella* by its smaller dental size, by the absence or weak development of molar cingula, and by the high degree of molarization in its premolar series (the lingually separated and nearly parallel protoloph and metaloph are present both on P^{3-4} and P^2) (Figure 4). This high degree of molarization in its premolar series suggests that *D. birmanica* is the most derived species among the genus *Deperetella*. Radinsky (1965), however, interpreted this fact as a result of a greater elongation of the anterior premolars in *Deperetella cristata* in contrast to the higher degree of molarization of the premolars in *Deperetella similis* (= *D. birmanica*).

The new synonymy enables us to correlate the Pondaung fauna with local middle to late Eocene mammal faunas in China, which yield *D. birmanica*, and Mongolia, which yield *D. sp. cf. D. birmanica*: Dongjun fauna of the Bose Basin, Guangxi Province, China; Lumeiyi fauna of the Lunan Basin and Xiangshan fauna of the Lijiang Basin, Yunnan Province, China; Heti fauna (from the Rencun Member) of the Yuanchu Basin, Shanxi and Henan Province, China; Huangzhuang fauna of Qufu County, Shandong Province, China; Ergilin Dzo fauna (from the Sevkul Member) of Khoer Dzan, Mongolia (Figure 1; Li and Ting, 1983; Russell and Zhai, 1987; Shi, 1989; Zong *et al.*, 1996; Dashzeveg and Hooker, 1997; Huang, 1999). The occurrences of *D. birmanica* and *D. sp. cf. D. birmanica* suggest that these deposits are roughly contemporaneous to each other, and that these mammal faunas were mutually interchanged among them during middle to late Eocene.

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Late Oligocene larger foraminifera from the Komahashi-Daini Seamount, Kyushu-Palau Ridge and their tectonic significance

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Abstract. A larger foraminiferal assemblage consisting of *Miogypsinella ubaghsi* (Tan), *Spiroclypeus margaritatus* (Schlumberger) and other species is described from limestone blocks dredged at two sites on the Komahashi-Daini Seamount of the Kyushu-Palau Ridge. The fauna dates the limestone samples as Late Oligocene and is correlatable with the younger part of the Minamizaki Limestone on the Ogasawara (Bonin) Islands. These shallow-water benthic foraminifera give evidence for the shallow-water attitude of the Kyushu-Palau Ridge during the Oligocene, which has been rifted, submerged, and finally subsided to the present water depth.

Key words: Komahashi-Daini Seamount, Kyushu-Palau Ridge, larger foraminifera, Late Oligocene

Introduction

The Kyushu-Palau Ridge is an about 3,000 km long submarine ridge with a general N-S trend which divides the sea floor into the Nankai Trough on the east and the Ryukyu Trench on the west (Figure 1). On the Kyushu-Palau Ridge, a series of isolated seamounts were discovered during the 1970's (Shiki *et al.*, 1974; Shiki *et al.*, 1975). The Komahashi-Daini Seamount is located near the northern margin of this ridge. During the R/V Tansei-Maru KT94-10 Cruise, which operated July 5-12, 1994, we dredged limestone samples along with many intrusive, hypabyssal and volcanic rocks such as tonalite, andesite, tuff and pumice from the Komahashi-Daini Seamount. In this study, we describe the larger foraminifera in the limestone samples and discuss the age assignment based on the foraminiferal data and their tectonic significance.

Material

During the KT94-10 cruise, samples were dredged at two sites of the Komahashi-Daini Seamount. DG-04 site is located on the northeastern slope of the north peak, and DG-05 site on the eastern slope of the major peak (Table 1 and Figure 2). Among the rock samples, one limestone sample (DG-04-01) from the northern site and two (DG-05-01 and DG-05-02) from the southern site were studied.

The limestone samples are indurated packstone or

packstone to wackstone. All these samples are moderately hard to compact, and white to creamy white in color. They contain abundant larger and smaller benthic foraminifera, together with coral biolithite, calcareous algae and mollusks.

All of the described larger foraminiferal specimens are kept in the Geological Survey of Japan, under catalogue numbers GSJF 15418 to GSJF 15427.

Results

Thirteen foraminiferal species were identified (Figures 3–8). Dominant species are *Spiroclypeus margaritatus*, *Nephrolepidina praejaponica*, *N. angulosa*, *N. marginata*, *Eulepidina ephippioides*, *Heterostegina borneensis*, *Miogypsinella ubaghsi* and *Austrorillina howchini*. No distinct difference in species composition was found among the three samples. This assemblage was assigned an age of Te 1–4 (Tertiary e 1–4) according to the system of Far East Letter Stages, equivalent to Late Oligocene (Hashimoto *et al.*, 1980; Hashimoto and Matsumaru, 1984; Mohiuddin, 1997). Coexistence of *M. ubaghsi* and *S. margaritatus* along with *H. borneensis*, *Eulepidina*, *Miogypsinoides* and *Spiroclypeus* is indicative of a Late Oligocene age as seen in the Melinau Limestone of Sarawak, North Borneo (Adams, 1965). Moreover, Adams and Belford (1974) suggested that the association of *S. margaritatus*, *H. borneensis* and *E. ephippioides* is indicative of the Tertiary lower e, which is believed to be equivalent to the Upper Oligocene (Chattian) of Europe.

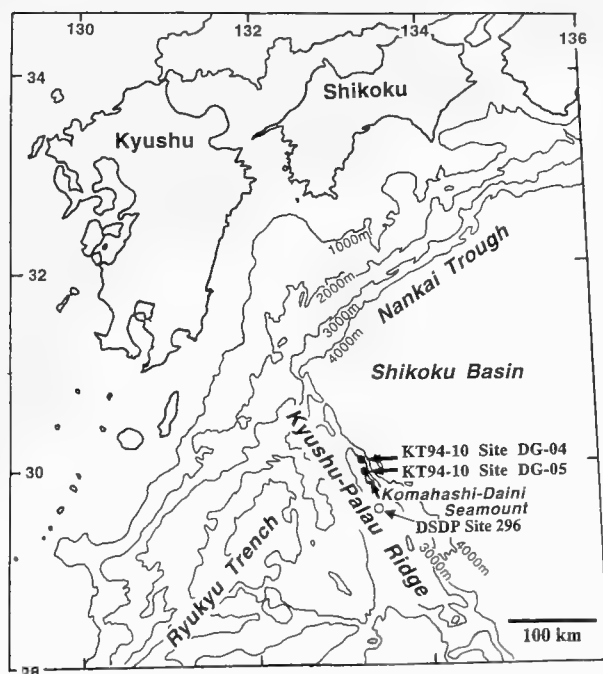


Figure 1. Index map of dredged samples used for this study.

The *M. ubaghsi*-*S. margaritatus* assemblage can be correlated with the fauna of the upper member of the Minamizaki Limestone in Chichi-Jima and Minami-Jima, Bonin Islands. *Miogypsinella boninensis* (Matsumaru, 1996) described from the Bonin Islands is thought to be a junior synonym of *Miogypsinella ubaghsi* (Tan, 1936). This assemblage may be correlated with the assemblage of Te Stage limestones from 1210 to 1599 feet depth in Enewetok Atoll Drill Hole and with those from 1597.5 to 1671 feet depth in Bikini Atoll Drill Hole. The *M. ubaghsi*-*S. margaritatus* assemblage is also correlated with the fauna of the Butoon Limestone, Mindoro, Philippines (Hashimoto and Matsumaru, 1984). The Te Stage is regarded as corresponding to Zone P. 21 of Blow's (1969, 1979) planktonic foraminiferal zonation.

Discussion

Konda (1975) reported larger foraminifera in limestone samples dredged from the eastern slope near a peak of the

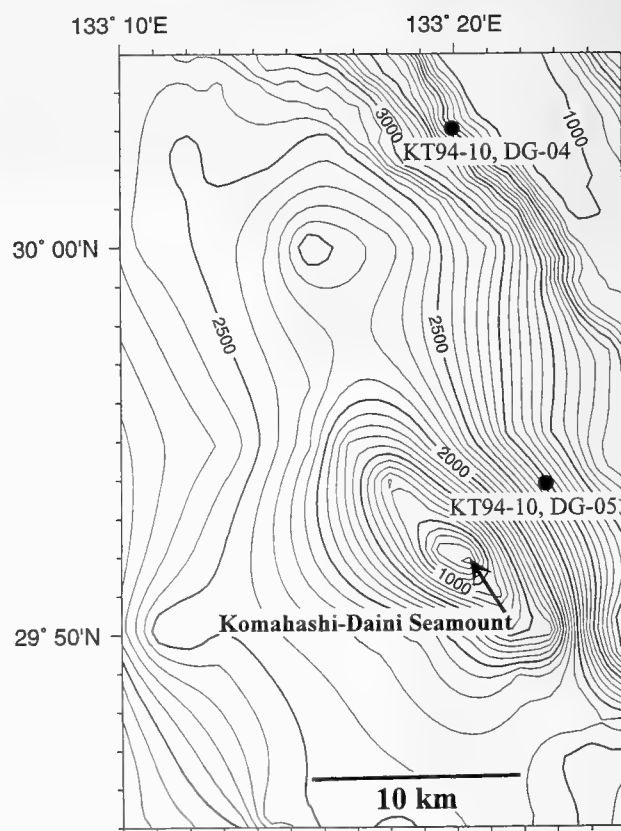


Figure 2. Location of dredge sites KT94-10 on Kyushu-Palau Ridge. Adopted from Ohara *et al.* (1999). Contours in meters.

Komahashi-Daini Seamount, Kyushu-Palau Ridge and assigned to the samples an age younger than Middle Miocene based on the foraminiferal assemblage. The northern half of the Kyushu-Palau Ridge was dated around 48 Ma by Ar-Ar dating of volcanoclastic and granitic rocks (Ozima *et al.*, 1977). A similar age was also obtained from K-Ar age of augite-orthopyroxene andesite rocks in Haha-Jima of the Bonin Islands (Kaneoka *et al.*, 1970). These age data suggest that the Izu-Ogasawara arc was juxtaposed with the northern Kyushu-Palau Ridge before the initiation of back-arc spreading in the Shikoku Basin. Moreover, larger foraminiferal age data in this study gave a Late Oligocene age for the limestone blocks of the Komahashi-Daini

Table 1. Location of dredged samples on the Kyushu-Palau Ridge.

| Sample No. | Location | Latitude | Hit bottom Longitude | Water depth (m) | Latitude | Off bottom Longitude | Water depth (m) | Dredged materials |
|-----------------------|-------------------------------|-------------|----------------------|-----------------|-------------|----------------------|-----------------|----------------------------------|
| DG-04-01 | KPR, Unnamed Seamount | 30°02.983'N | 133°19.880'E | 3800 | 30°02.074'E | 133°18.465'E | 2632 | tuff, pumice and limestone |
| DG-05-01 and DG-05-02 | KPR, Komahashi-Daini Seamount | 29°53.983'N | 133°22.656'E | 3334 | 29°53.160'N | 133°20.992'E | 2500 | tonalite, andesite and limestone |

| Sample No. | | | Larger foraminiferal species |
|------------|----------|----------|---|
| DG-04-01 | DG-05-01 | DG-05-02 | |
| X | X | X | <i>Spiroclypeus margaritatus</i> (Schlumberger) |
| X | X | | <i>Heterostegina borneensis</i> van der Vlerk |
| X | X | | <i>Nephrolepidina praejaponica</i> Matsumaru |
| X | X | | <i>Nephrolepidina angulosa</i> (Provale) |
| X | X | | <i>Nephrolepidina marginata</i> (Michelotti) |
| X | | X | <i>Miogypsinella ubaghsi</i> (Tan) |
| X | | X | <i>Austrotrillina howchini</i> (Schlumberger) |
| X | | | <i>Eulepidina dilatata</i> (Michelotti) |
| | X | X | <i>Eulepidina ehippioides</i> (Jones and Chapman) |
| | X | | <i>Amphistegina radiata</i> (Fichtel and Moll) |
| X | | | <i>Eulepidina</i> sp. |
| X | | | <i>Ammonia</i> sp. |
| X | | X | <i>Heterostegina</i> sp. |

Figure 3. Occurrence of larger foraminiferal species in dredged samples.

Seamount, which is consistent with the oldest age of the basement rocks in the Shikoku Basin (Watts and Weissel, 1975).

The association of Late Oligocene coral-bearing limestone with benthic foraminifera of shallow-sea nature and igneous rocks recognized at the Komahashi-Daini Seamount has also been reported at DSDP Site 296, south of the seamount, at a depth of 2,920m (Figure 1). This evidence suggests that volcanogenic-calcareous sedimentary sequences of Oligocene age are rather widely distributed in the northern part of the Kyushu-Palau Ridge, including the Komahashi-Daini Seamount.

In view of the paleoenvironmental nature of the larger foraminiferal assemblage consisting of *Miogypsinella*, *Spiroclypeus*, *Austrotrillina*, *Eulepidina*, *Amphistegina* and *Heterostegina*, an environment of the shallow open ocean at the shelf edge was suggested for the deposition of limestone beds of the Komahashi-Daini Seamount, as in the case of the limestone beds of the Minamizaki Limestone, Chichi-Jima (Matsumaru, 1996). Moreover, the presence of several species of *Lepidocyclina* (*Eulepidina*) associated with pyroclastic sediments in cores 56 and 57 at DSDP Site 296 indicates a neritic environment (Ujiié, 1975).

In contrast to the cases of the Komahashi-Daini Seamount and of Chichi-Jima, where the Late Oligocene sediments are exposed near the seamount surface, a drill hole at DSDP Site 296 displays a considerably continuous sequence from in situ volcanic rocks through Late Oligocene shallow-water sediments. It includes larger foraminifera and pelagic calcareous ooze, suggesting a subsidence of the Kyushu-Palau Ridge (Ujiié, 1975).

It is noteworthy that the northern parts of the Kyushu-Palau Ridge and the Izu-Bonin Arc resemble each other in the timing of the cessation of volcanic activity and in the final

paleoenvironment reaching a shallow-water depth. Since Uyeda and Ben-Avraham (1972) many authors have supposed that both ridges formed a single arc at the initial stage and then were divided into two arcs owing to the spreading of the Shikoku and Parece Vella Basins. This study offers a new line of supporting evidence for this hypothesis.

Conclusion

The oldest age of the Kyushu-Palau Ridge is Late Oligocene based on larger foraminifera. The benthic foraminiferal assemblage in the limestone samples is correlated with that from the upper part of the Minamizaki Limestone exposed on the Ogasawara (Bonin) Islands of the Izu-Bonin Arc. This fact suggests that the Kyushu-Palau Ridge and the Izu-Bonin Arc initially formed a single arc. Afterward the arc may have split by a spreading of the Shikoku and Parece Vella Basins.

Systematic descriptions

Family Lepidocyclinidae Scheffen, 1932

Genus *Nephrolepidina* Douvillé, 1911

Nephrolepidina praejaponica Matsumaru, 1989

Figures 6.1–6.4, 6.6, 6.7, 6.9, 6.10, 7.1, 7.6–7.9

Nephrolepidina praejaponica Matsumaru. In Matsumaru and Kimura, 1989, p. 265, 267, figs. 6.1–6.13; Matsumaru *et al.*, 1993, p. 8, figs. 2.4, 3.6–3.8.

Material.—Thirteen specimens (GSJF 15420–1–13) including one megalospheric specimen in a vertical section (GSJF 15420–1; Figure 6.1).

Description.—Tests of megalospheric specimens, GSJF

15420–1–8, are small lenticular with diameter of 3.5 to 5.5 mm and thickness of 1.5 to 2 mm. Conical pillars are from 80 μ m to 100 μ m in diameter, and distributed in the central part of the test surface. The embryonic chambers are of nephrolepidine type. The protoconch is subcircular with a diameter of 240 μ m. The second large chamber, the deutoconch embraces the protoconch and has an internal diameter of 320 μ m. The ratio of the inner diameter of the deutoconch (II) to that of the protoconch (I) is 1.3. The outer wall of the embryonic chambers is more than 25 mm thick. The equatorial chambers of arcuate form near the peribryonic chambers change from ogival to short hexagonal near the periphery. The height of the equatorial layer near the center is about 200 μ m and at the periphery less than 100 μ m. The lateral chambers are rectangular in shape and are arranged in a tier of 10 to 12 layers over the center. Chambers over the central area of the test have a length of more than 160 to 200 μ m, a height of 45 to 60 μ m, and floors and roofs 20 to 25 μ m thick.

Remarks.—The present specimen has the same features of small embryonic chambers and short hexagonal equatorial chambers in as *N. praejaponica* Matsumaru from the Lower Member of the Misaki Formation, Tosa Shimizu City, Kochi Prefecture, Shikoku (Matsumaru and Kimura, 1989) and the Early Miocene (Aquitian) Shimizu Formation (Matsumaru *et al.*, 1993), Shikoku Island. *Nephrolepidina praejaponica* is similar to *N. japonica* (Yabe) in overall morphology, but differs from the latter in having a small test and small embryonic chambers, primitive form of the embryonic chambers, short hexagonal equatorial chambers, rectangular lateral chambers and wavy floors and roofs.

Nephrolepidina species have been reported from Zones N. 8 and N. 9 of Blow (1969) in the Japanese mainland (Yabe, 1906; Yabe and Hanzawa, 1922; Hanzawa, 1931a, b; 1964; Matsumaru, 1967, 1971a) except the Izu Peninsula and Shikoku Island (Matsumaru, 1971a; Matsumaru and Kimura, 1989).

Nephrolepidina angulosa (Provale, 1909)

Figure 6.5

Lepidocyclus tournoueri Lemoine and R. Douvillé var. *angulosa* Provale, 1909, p. 28, pl. 3, figs. 13–15.

Lepidocyclus angulosa Provale. Rutten, 1912, p. 21, figs. 1–4.

Lepidocyclus (Nephrolepidina) angulosa Provale. Hanzawa, 1957, p. 76, 77, pl. 20, figs. 1–9, pl. 21, fig. 5, pl. 22, figs. 4, 14.

Nephrolepidina angulosa (Provale). Matsumaru, 1992, p. 259, 260, figs. 1.6, 1.7.

Material.—One megalospheric specimen in a vertical section, GSJF 15421.

Remarks.—This species is characterized by having a flat-

topped central boss with stout pillars; equatorial chambers in the mature stage are hexagonal in shape; the roof and floor of the lateral chambers are straight; and the chamber cavities are narrow and long. External appearance of the shell is similar to that of *Nephrolepidina praejaponica* Matsumaru, but it differs from the latter in possessing several conical pillars formed on the flat top of the central boss.

Family Nummulitidae de Blainville, 1827

Genus *Spiroclypeus* H. Douvillé, 1905

Spiroclypeus margaritatus (Schlumberger, 1902)

Figures 4.1, 4.2, 4.4, 4.5, 4.7, 4.9, 4.10, 5.1–5.13, 8.1

Heterostegina margaritata Schlumberger, 1902, p. 152, 153, pl. 7, fig. 4.

Spiroclypeus orbitoides H. Douvillé, 1905, p. 460–462, pl. 14, figs. 1–6; Tan, 1937, p. 183, 184, pl. 1, figs. 2–4, pl. 2, figs. 1–13, pl. 3, figs. 1–7; Cole, 1957a, p. 332–333, pl. 95, figs. 6–12; Matsumaru, 1976a, p. 200, pl. 1, figs. 1, 8, 10; Hashimoto, Matsumaru and Sugaya, 1981, p. 59, pl. 13, fig. 8.

Spiroclypeus leupoldi van der Vlerk, 1925, p. 14, 15, pl. 2, fig. 16; pl. 5, figs. 41, 48; Yabe and Hanzawa, 1929, p. 188, pl. 24, fig. 9; Cole, 1954, p. 577, 578, pl. 208, figs. 1–19; Hanzawa, 1957, p. 45, 46, pl. 5, figs. 7–13; Matsumaru, 1974, p. 108, pl. 15, figs. 1–4, 10, 13–15, 21–23, 28; Matsumaru, 1976a, p. 199, 200, pl. 1, figs. 4–7, 14, 15, 21, 23, 4.

Spiroclypeus yabei van der Vlerk, 1925, p. 16, pl. 2, fig. 19, pl. 5, figs. 40, 50; Tan, 1937, p. 183, pl. 1, figs. 5, 6, pl. 3, figs. 10, 11, pl. 4, figs. 8–10, text-fig. 1; Cole, 1954, p. 580–581, pl. 207, figs. 1–14, pl. 208, figs. 20–26; Cole, 1957b, p. 764, pl. 239, figs. 9–10.

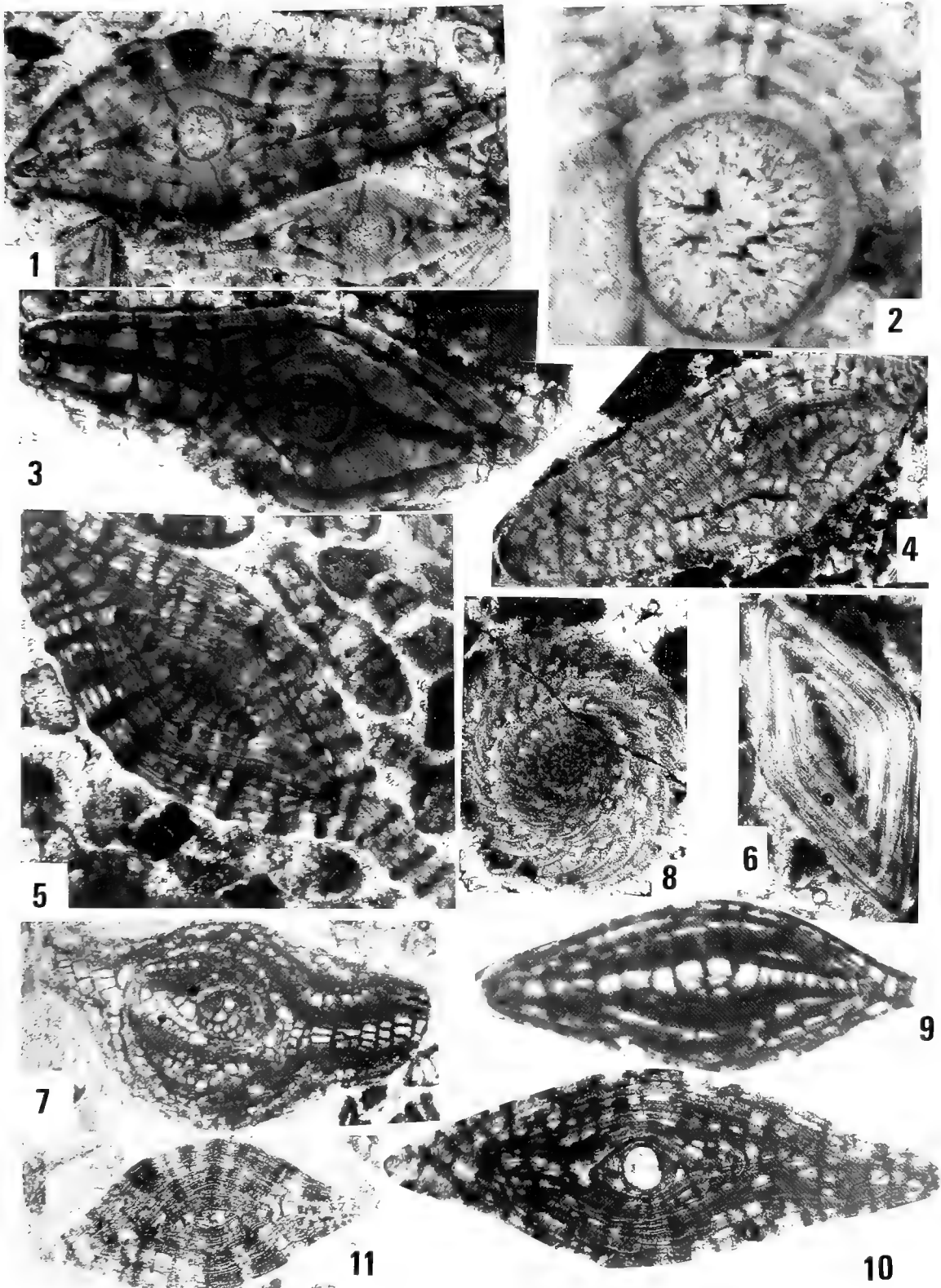
Spiroclypeus tidoenganensis van der Vlerk, 1925, p. 16, 17, pl. 1, fig. 12, pl. 5, figs. 42, 47; Tan, 1937, p. 183, pl. 1, fig. 10, pl. 2, figs. 4–5, pl. 3, fig. 12, pl. 4, figs. 2–5, 19–21; Hanzawa, 1957, p. 46, 47, pl. 3, figs. 1–6, pl. 4, figs. 1, 8–10; Cole, 1957a, p. 332, pl. 95, figs. 13–15; Matsumaru, 1976a, p. 200, pl. 1, figs. 3, 9, 12, 18–20, 22, pl. 6, fig. 15; Hashimoto, Matsumaru and Sugaya, 1981, p. 60, 61, pl. 13, figs. 9, 12.

Spiroclypeus margaritata (Schlumberger). Yabe and Hanzawa, 1925, p. 627–630, pl. 2, fig. 10, pl. 3, figs. 8, 9, pl. 4, figs. 3–8, text-figs. 1–4; Krijnen, 1931, p. 89, pl. 1, figs. 1–3; Tan, 1937, p. 182, 183, pl. 2, fig. 12, pl. 3, fig. 9, pl. 4, figs. 6, 7; Hanzawa, 1940, p. 789, 790, pl. 42, figs. 3–9; Cole, 1954, p. 578–580, pl. 206, figs. 10–25, pl. 207, figs. 15, 16; Matsumaru, 1974, p. 108, pl. 15, figs. 16, 24, 26; Hashimoto and Matsumaru, 1975, p. 122, pl. 13, figs. 11, 12; Hashimoto, Matsumaru and Sugaya, 1981, p. 59, 60, pl. 13, fig. 3; Matsumaru, Myint Thein and Ogawa, 1993, p. 10, 11, figs. 2–1–9, 3–1.

Spiroclypeus margaritata (Schlumberger) var. *umbonata* Yabe and Hanzawa, 1929, p. 187, 188, pl. 124, figs. 5–8.

Spiroclypeus higginsii Cole. Hanzawa, 1957, p. 45, pl. 5, figs. 1–6, 14; Cole, 1957a, p. 332, pl. 95, figs. 1–5, pl. 109, fig. 16; Cole,

→ **Figure 4.** 1, 2, 4, 5, 7, 9, 10. *Spiroclypeus margaritatus* (Schlumberger), 1 (upper), 5, 9, 10: vertical sections, x 30, (GSJF 15418–1–4) 4, 7: oblique sections, x 30, (GSJF 15418–5–6) 2: megalospheric protoconch x 200, (GSJF 15418–7). 3. *Heterostegina* sp. vertical section, x 30. 6, 8. *Amphistegina radiata* (Fichtel and Moll), 6: vertical section, x 20, (GSJF 15427–1) 8: median section, x 20, (GSJF 15427–2) 11. *Heterostegina borneensis* van der Vlerk, vertical section, x 30, (GSJF 15419).



1957b, p. 763, 764, pl. 239, figs. 11, 12, 14; Matsumaru, 1974, p. 108, pl. 15, figs. 1, 5, 8, 12, 18, 19; Matsumaru, 1976a, p. 199, pl. 1, figs. 2, 11, 16, 17.

Spiroclypeus margaritatus (Schlumberger). Matsumaru, 1996, p. 104–108, pl. 32, figs. 1–8, pl. 33, figs. 1–9.

Material.—Twenty specimens, GSJF 15418–1–20.

Description.—Test small, inflated to lenticular, bordered by a rather thin flange, central area more than 3.5 mm in diameter and 1.5 mm in thickness. Low raised pustules distributed in umbonal portion of the test having a diameter of less than 100 μ m. The megalospheric embryonic chambers consist of a spherical protoconch followed by a reniform deutoconch. The inner diameters of protoconch (DI) and deutoconch (DII) vary from 200 to 250 μ m and 450 to 550 μ m, respectively with a (DII/DI) ratio of 2.2.

Remarks.—Tan (1937) divided the species of *Spiroclypeus* into the pustulate and the reticulate group. The former group is characterized by prominent pillars on the umbonal portion of the test, the later one by the development of an external reticulation of the septa at the central part of the test. *Spiroclypeus margaritatus* belongs to the pustulate group and is characterized by large and heavy pillars, thick roofs and floors in lateral chambers, and moderate sized operculine chambers.

According to Matsumaru (1996), all the *Spiroclypeus* species reported from the West Pacific region are junior synonyms of *Spiroclypeus margaritatus* (Schlumberger). This species, known from Chichi-Jima, is restricted in occurrence to the Upper Member of the Minamizaki Limestone. It has a comparatively short stratigraphic range in Te, from the top of the *Heterostegina borneensis* Zone to the base of the *Miogypsinoides dehaartii* Zone, in the Eniwetok Atoll Drill Holes (Cole, 1957b).

Genus *Heterostegina* d'Orbigny, 1826

Heterostegina borneensis van der Vlerk, 1929

Figure 4.11

Heterostegina borneensis van der Vlerk, 1929, p. 16, figs. 6a–c, 25a–b; Cole and Bridge, 1953, p. 23, pl. 2, figs. 1–3, 5; pl. 4, figs. 16–18; Hanzawa, 1957, p. 95, pl. 26, figs. 11, 19; pl. 27, figs. 4–8; Matsumaru, 1976a, p. 199, pl. 3, figs. 17–19, 21–22; Matsumaru, 1996, p. 94–96, pl. 28, figs. 1–7.

Material.—One microspheric specimen in a vertical section, GSJF 15419.

Description.—Test small, initial part evenly lenticular with a moderately wide, thin flange on distal part. Test diameter ranges from 2.2 mm to 2.7 mm; test thickness ranges from 1.0 to 1.2 mm; thickness of pillars varies from 120 μ m at umbo to 100 μ m at tip of flange. In vertical section, embryonic apparatus biloculine; initial protoconch subcircular; its diameter less than 100 μ m. Prominent pillars are present on the central boss of the test. Pillars penetrating to outer

wall of embryonic apparatus and equatorial layer.

Remarks.—*Heterostegina borneensis* and *Spiroclypeus margaritatus* co-occur in the Lower and Upper members of the Minaminizaki Limestone. In the Komahashi-Daini Seamount Limestone, *H. borneensis* is associated with *Spiroclypeus margaritatus*, the latter species being the more abundant one. *H. borneensis* has also been recognized as a marker species to distinguish Te1–4 from Te5 (Cole, 1957a; Adams, 1965; Matsumaru, 1974, 1978), since van der Vlerk (1925) regarded it to be a useful species for delimiting Te1–4.

Family Austrotrillinidae Loeblich and Tappan, 1986

Genus *Austrotrillina* Parr, 1942

Austrotrillina howchini (Schlumberger, 1893)

Figure 8.11

Trillina howchini Schlumberger, 1893, p. 119, 120, text-figs. 1–2, pl. 3, fig. 6; Hanzawa, 1940, p. 791–793, pl. 42, figs. 1, 2.

Austrotrillina howchini (Schlumberger). Cole and Bridge, 1953, p. 20, pl. 14, fig. 12; Cole, 1954, p. 573, pl. 210, figs. 6–9; Hanzawa, 1957, p. 38, pl. 22, figs. 12, 13; pl. 34, figs. 1, 2; Matsumaru, 1996, p. 214–216, pl. 84, figs. 3–7.

Material.—One microspheric specimen in a longitudinal section, GSJF 15424.

Remarks.—*Austrotrillina howchini* originally described from Saipan is also found in the Bikini Atoll Drill Holes associated with *Spiroclypeus* and *Eulepidina* in Te Stage (Cole, 1954). The stratigraphic range of this species has been given as Te through Tf1–2 (Glaessner, 1943) and as Te and Tf1 (van der Vlerk, 1948). Hanzawa (1940) stated that this species is found only in the Aquitanian stage in the Western Pacific. Hashimoto and Matsumaru (1984) suggested that *A. howchini* ranged from Te4 to Te5–Tf1. This species occurs in association with *Miogypsinella boninensis* and *Spiroclypeus margaritatus* in the Minamizaki Limestone, Chichi-Jima, assigned to Te 1–4 of the Far East Letter Stages (Hashimoto *et al.*, 1980; Hashimoto and Matsumaru, 1984).

Family Lepidocyclinidae Scheffen, 1932

Subfamily Eulepidininae Matsumaru, 1991

Genus *Eulepidina* H. Douvillé, 1911

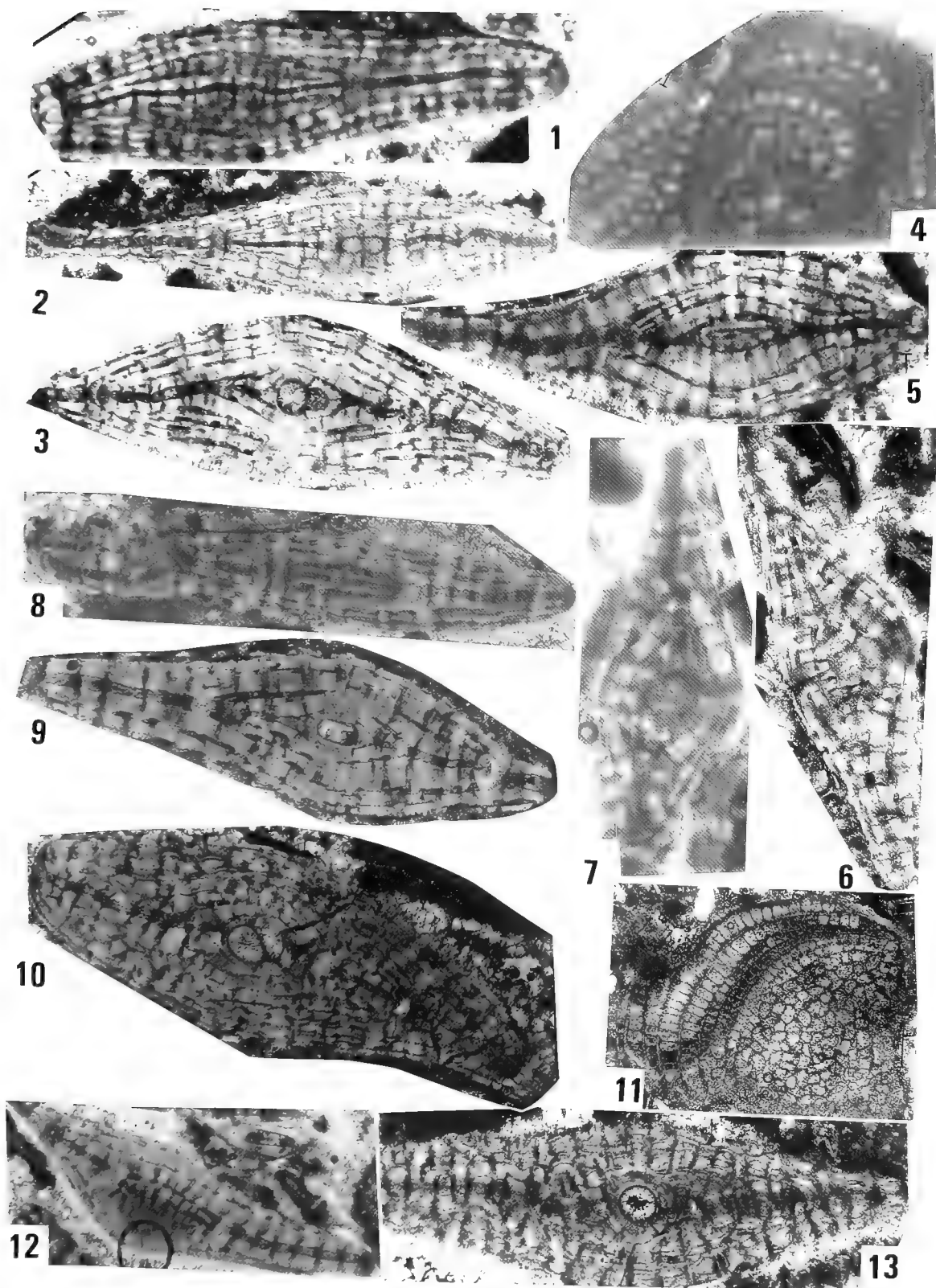
Eulepidina ehippioides (Jones and Chapman, 1900)

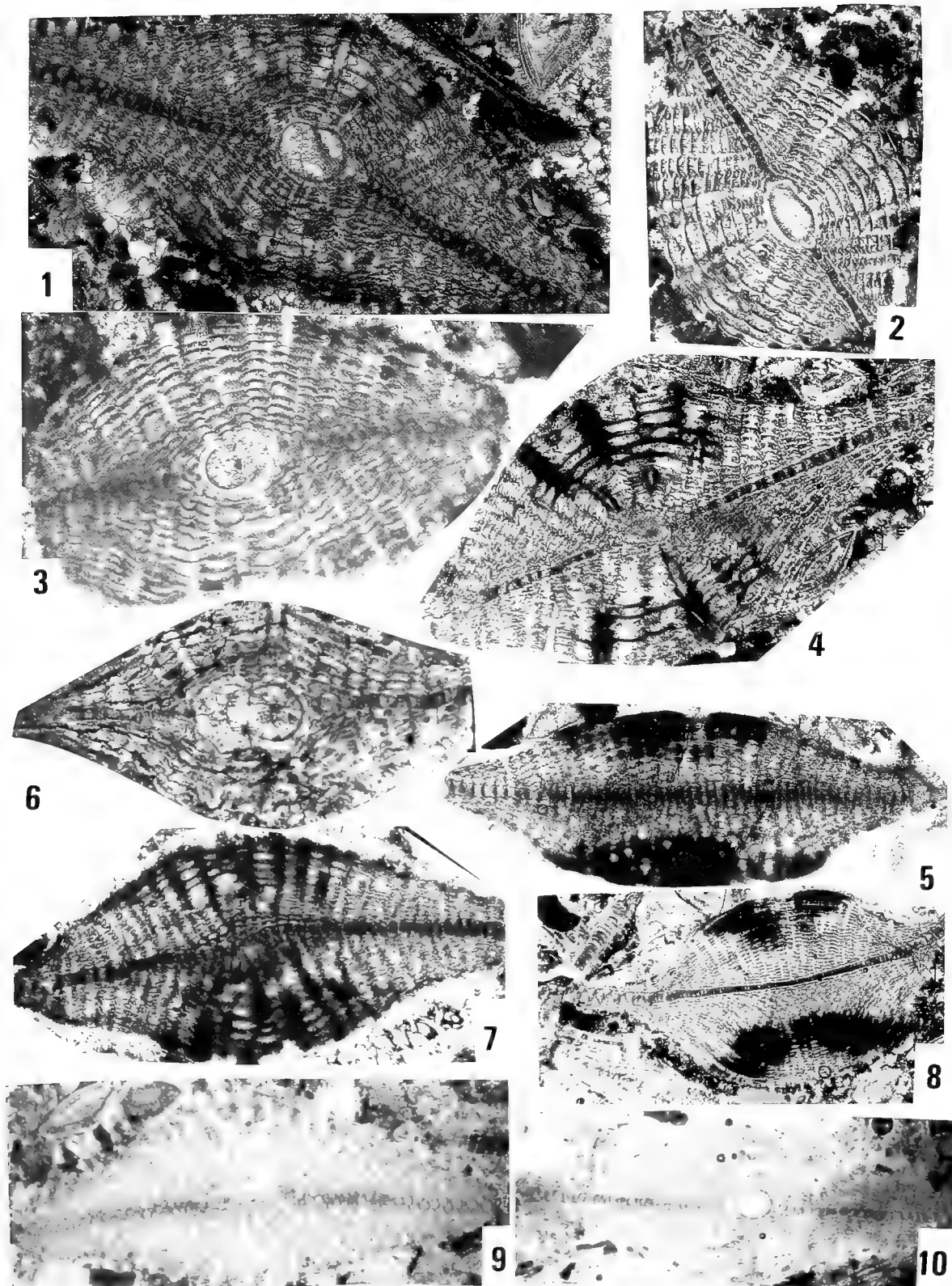
Figures 6.8, 7.3, 7.4

Orbitoides (*Lepidocyclina*) *ehippioides* Jones and Chapman, 1900, p. 251, 252, pl. 20, fig. 9. *Lepidocyclina ehippioides* Jones and Chapman. Grimsdale, 1952, p. 240–244, pl. 23, figs. 8, 17, 18. *Lepidocyclina* (*Eulepidina*) *formosa* Schlumberger. Cole, 1954, p. 594–597, pl. 216, figs. 1–16; pl. 217, figs. 9–11, pl. 218, figs. 1, 3, 4.

Lepidocyclina (*Eulepidina*) *gibbosa* Yabe. Cole, 1954, p. 597, pl. 217, figs. 9–11.

➔ **Figure 5.** 1–13. *Spiroclypeus margaritatus* (Schlumberger). 1–3, 5–10, 12, 13: vertical sections, x 30, (GSJF 15418–8–18), 4, 11: oblique sections, x 30, (GSJF 15418–19–20).





Lepidocyclina (*Eulepidina*) *planata* Oppenoorth. Cole, 1954, p. 597, 598, pl. 217, figs. 7, 8; pl. 218, figs. 5, 6.

Lepidocyclina (*Eulepidina*) *ephippioides* Jones and Chapman. Cole, 1957b, p. 346–337, pl. 108, figs. 4–13; pl. 109, figs. 11–15.

Eulepidina ephippoides (Jones and Chapman). Matsumaru, 1996, p. 178–181, pl. 65, figs. 1–6, pl. 66, figs. 1–3; pl. 67, figs. 1–6; pl. 68, figs. 1–3; pl. 69, figs. 1–4; pl. 70, figs. 1–5, text-fig. 20–5.

Material.—Three megalospheric specimens (GSJF 15426–1–3).

Remarks.—*Eulepidina ephippoides* is characterized by the possession of a small nucleoconch and hexagonal or spatulate equatorial chambers. The earliest name of this species was thought to be *Orbitoides* (*Lepidocyclina*) *ephippioides* Jones and Chapman. According to Grimsdale (1952), the American Oligocene species *L. (E.) favosa* Cushman should be a synonym of *L. ephippoides* (Jones and Chapman).

***Eulepidina dilatata* (Michelotti, 1861)**

Figure 8.1 (lower)

Orbitoides dilatata Michelotti, 1861, p. 17, pl. 1, figs. 1–2.

Eulepidina dilatata (Michelotti). Matsumaru, 1971b, p. 184, 185, pl. 22, figs. 28–38; Hashimoto and Matsumaru, 1975, p. 114, 115, pl. 12, figs. 10, 11; Matsumaru, 1996, p. 162–178, pl. 60, figs. 1–6; pl. 61, figs. 1–6; pl. 62, figs. 1–7; pl. 63, figs. 1–6; pl. 64, figs. 1–2, text-figs. 20–2, 4, text-fig. 30.

Material.—One obliquely sectioned megalospheric specimen, GSJF 15425.

Remarks.—The present species is characterized by having a lenticular shape, polygonal outline, large nucleoconch, hexagonal equatorial chambers, low and long lateral chambers and thin roofs and floors. It differs in general shell shape from *Eulepidina ephippoides* (Jones and Chapman). Recently, Matsumaru (1996) investigated the size of the embryonic chambers of *E. dilatata* and *E. ephippoides* from the Minamizaki Limestone, Chichi-Jima and concluded that microspheric *E. dilatata* slightly differs in chamber budding formation from microspheric *E. ephippoides*.

Family Miogypsinidae Vaughan, 1928

Genus ***Miogypsinella*** Hanzawa, 1940

***Miogypsinella ubaghsi* (Tan, 1936)**

Figures 7.2, 8.2, 8.3

Miogypsinoides ubaghsi Tan, 1936, p. 47, 48, pl. 1, figs. 1–7; Cole, 1954, p. 603, 604, pl. 221, figs. 5, 9–18; pl. 222, figs. 13, 15.

Miogypsinella ubaghsi (Tan). Hanzawa, 1940, p. 767, 768, text-fig. 4.

Material.—Three melalospheric specimens; one in an

equatorial section, GSJF 15423–3 (Figure 8.3), one in an axial section, GSJF 15423–1 (Figure 8.2), and one in a vertical section, GSJF 15423–2 (Figure 8.2).

Description.—Test small, slightly wider than long, fan-shaped; 1.5 to 1.8 mm in diameter and 0.65 to 0.75 mm in thickness. Surface ornamentation consists of large pustules over the initial portion and finer, closer-spaced pustules over the distal portion. Embryonic chambers are bilocular, first chamber is nearly spherical and second chamber is reniform. Initial chambers are followed by subquadrate periembrionic chambers arranged so that they form virtually two coils. Periembrionic chambers gradually increase in length as they are added for about 1.5 volutions at which point they decrease gradually in length to the end of the coil.

Remarks.—The present species differs from *Miogypsinella borodinensis* Matsumaru, 1996, described from Minamizaki Limestone, Chichi-Jima, in having fewer equatorial and embryonic chambers and a small apical angle.

Family Amphisteginidae Cushman, 1927

Genus ***Amphistegina*** d'Orbigny, 1826

***Amphistegina radiata* (Fichtel and Moll, 1798)**

Figures 4.6, 4.8, 8.1

Nautilus radiatus Fichtel and Moll, 1798, p. 58, pl. 8, figs. 8a–d.

Amphistegina lessoni d'Orbigny. Yabe and Hanzawa, 1925, p. 48, 49, pl. 8, figs. 9, 10; Hanzawa, 1931b, p. 156, pl. 24, fig. 7; pl. 25, figs. 5–8; pl. 10, fig. 4.

Amphistegina radiata (Fichtel and Moll). Yabe and Hanzawa, 1929, p. 179, 180, pl. 18, fig. 6; Matsumaru, 1976b, p. 408, pl. 1, figs. 1–3, 5–13, 17, 23, 26–27, text-figs. 6–8. Matsumaru, 1996, p. 188, pl. 74, figs. 1–5.

Material.—Three microspheric specimens (GSJF 15427–1–3)

Remarks.—The present specimens show a close similarity with those of *A. radiata* described from the Minamizaki Limestones (Matsumaru, 1996) and are characterized by many chambers in the last whorl, curvature of the spiral suture and septa and a large protoconch.

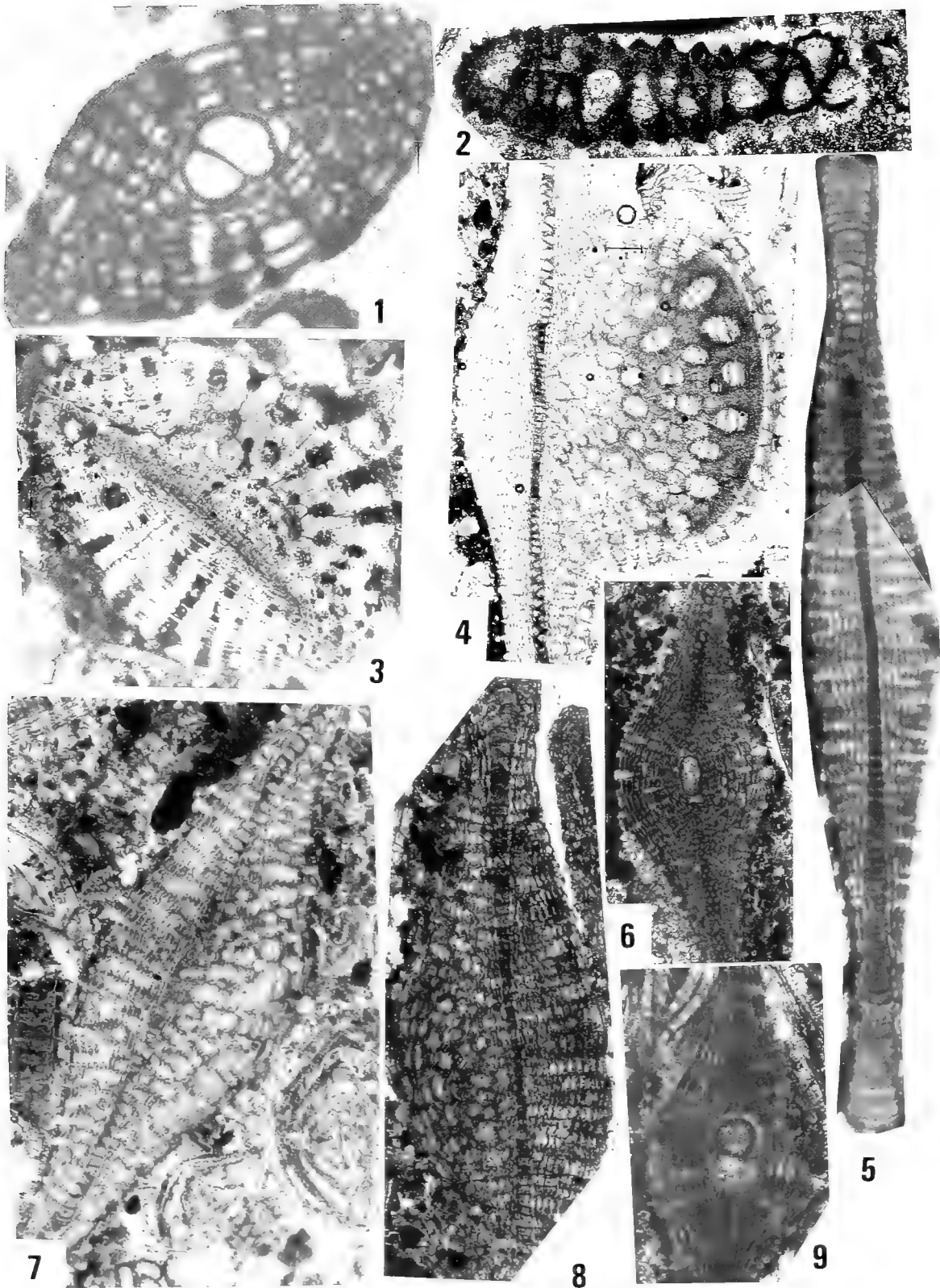
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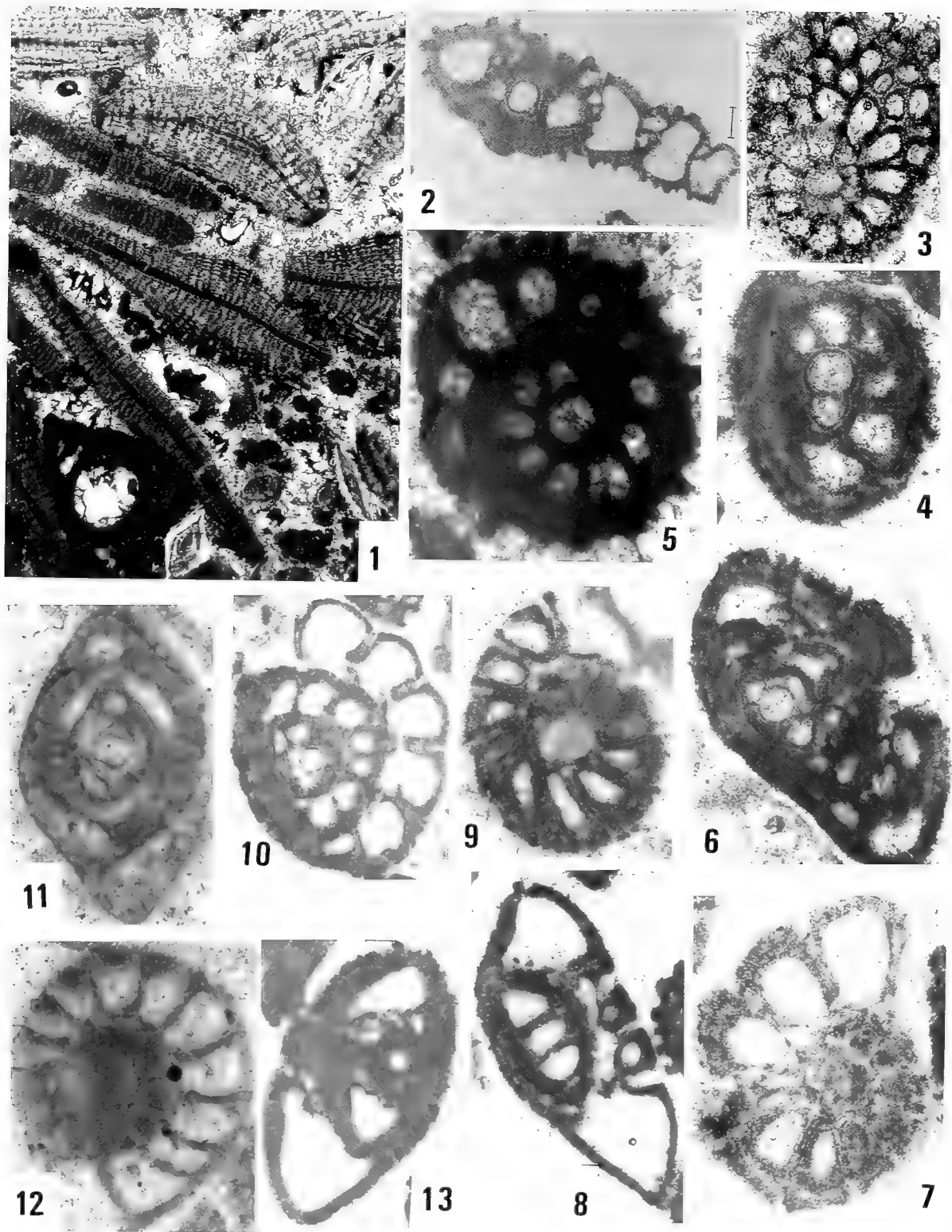
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← **Figure 6.** 1–4, 6, 7, 9, 10. *Nephrolepidina praejaponica* Matsumaru, vertical sections, x 30, (GSJF 15420–1–8). 5. *Nephrolepidina angulosa* (Provale), vertical section, x 30, (GSJF 15421). 8. *Eulepidina ephippoides* (Jones and Chapman), vertical section, x 20, (GSJF 15426–1).



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◀ **Figure 7.** 1, 6–9. *Nephrolepidina praejaponica* Matsumaru, 1: oblique section, x 20, 6–9: vertical sections, x 30, (GSJF 15420–9—13). 2. *Miogypsinnella ubaghsi* (Tan), vertical section, x 80, (GSJF 15423–1). 3, 4. *Eulepidina ehippioides* (Jones and Chapman), vertical sections, x 20, (GSJF 15426–2—3). 5. *Eulepidina* sp., vertical section, x 10.



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← **Figure 8.** 1. Bioclastic packstone containing diagnostic species such as *Spiroclypeus margaritatus* (Schlumberger) (GSJF 15418–20), *Nephrolepidina marginata* (Michelotti) (GSJF 15422), *Eulepidina dilatata* (Michelotti) (GSJF 15425) and *Amphistegina radiata* (Fichtel and Moll) (GSJF 15427–3) x 20. 2, 3. *Miogypsinella ubaghsi* (Tan). 2: axial section, x 20, GSJF 15423–2, 3: equatorial section, x 20, (GSJF 15423–3). 4–10, 12, 13. *Ammonia* sp., 4, 7, 9, 10, 12: oblique sections, x 20, 5: equatorial section, x 20, 6, 8, 13: axial sections, x 20. 11. *Austrotrillina howchini* (Schlumberger), longitudinal section, x 20, (GSJF 15424).

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***Kheraicer*as Spath (Ammonoidea)—new forms and records from the Middle Jurassic sequence of the Indian Subcontinent**

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Abstract. *Kheraicer*as Spath reached its peak during the Late Bathonian–Early Callovian and achieved a wide biogeographic distribution during that interval. The genus speciated rapidly and is represented in the fossil record by many species. The present endeavour provides a full taxonomic account of six species, of which five are from Kutch, western India. The sixth, *K. noetlingi* sp. nov., is based on the specimen described as ‘*Sphaeroceras*’ cf. *bullatum* d’Orbigny by Noetling (1896) from Baluchistan, Pakistan. Among the five Kutch species one has also been found in Baluchistan. We know little about specific dimorphism in *Kheraicer*as. In at least three instances dimorphic pairs have been matched. Of the six species of *Kheraicer*as described herein three are new and two are new records. They are: *Kheraicer*as *cosmopolitum*, *K. bullatum*, *K. cf. hannoveranum*, *K. spathi* sp. nov., *K. sp. A*, and *K. noetlingi* sp. nov. Like many other biota, including other ammonites, *Kheraicer*as speciation is marked by a high degree of endemism in the Kutch Sea, which extended up to Baluchistan. The endemism in this newly opened basin is due to the transgressions resulting from the fragmentation of Gondwanaland.

Key words: *endemism*, *Indian Subcontinent*, *Kheraicer*as, *Middle Jurassic*, *migration*, *sexual dimorphism*

Introduction

The genus *Kheraicer*as Spath, 1924 of the family Tuliidae has been thought to evolve from *Bullatimorphites* Buckman, 1921. Unlike its probable ancestor, *Kheraicer*as has a wide biogeographic distribution along the margins of the Tethys and the Pacific including Indonesia, Mexico and South America (Donovan *et al.*, 1981; Mangold, 1984; Riccardi *et al.*, 1989; Sandoval *et al.*, 1990; Westermann, 1993). The genus has not been reported, however, from the Boreal or Subboreal Provinces. From the distribution patterns it appears that *Kheraicer*as is longitudinally widespread and latitudinally more restricted to the palaeotropics and subtropics (see also Westermann and Callomon, 1988). It shows strong facies control, since most of its species are found mainly in calcareous facies deposited in shallow seas (Arkell, 1952; Bardhan *et al.*, 1988). *Kheraicer*as is of great stratigraphic value because of its short temporal distribution, although its biostratigraphic potentialities have not been fully explored (see Bardhan *et al.*, 1999). *Kheraicer*as ranges in age from Late Bathonian to Late Callovian (Hahn, 1969, 1971), but was at its peak during the Late Bathonian and Early Callovian when many other biostratigraphically impor-

tant taxa, e.g. *Macrocephalites* Zittel, 1884 and *Reineckeia* Bayle, 1878 also flourished.

In the present endeavour, we have made a taxonomic study of six *Kheraicer*as species, among which three are new and two have not been described previously from the subcontinent. Dimorphism is now considered to be very important in understanding evolution within a lineage and must be taken into account in phylogeny. Although dimorphism in *Kheraicer*as is evident, little is known about specific dimorphic pairs (for details see Bardhan *et al.*, 1994, 1999). In the present study we have distinguished dimorphic pairs in three species. Besides, there are two new microconchs and one macroconch species whose counterparts are still unknown. So far *Kheraicer*as is described in the literature mainly by macroconchs and microconchs are often rare. We have plentiful microconch specimens with a well preserved peristome showing apertural modifications. They are described herein.

The measurements of the types and other specimens of the present collection (abbreviated as below) are in mm. D=diameter; H=whorl height; W=whorl width; U=umbilical diameter.

Repository.—Curatorial Division, Geological Survey of

India, Calcutta (GSI); The Indian Museum, Calcutta; Department of Geological Sciences, Jadavpur University, Calcutta, India (JUM).

Previous Study

There are only a few reports of *Kheraicer* from the Indian subcontinent. Waagen's (1875) "*Stephanoceras bullatum*" d'Orbigny, 1846 which Spath (1924) subsequently made the type species of *Kheraicer*, i.e., *K. cosmopolitum*, comes from the Golden Oolite of Keera, Kutch. Recently many specimens of this species have been collected from Kutch, and the intraspecific variability and dimorphism of this species have been firmly established (Bardhan *et al.*, 1994). Noetting (1896) described a large single specimen as '*Sphaeroceras*' cf. *bullatum* (pl. 6, figs. 2, 2a) from the Polyphemus Limestone bed of Mazardrik, Baluchistan. Although it resembles *Kheraicer hannoveranum* (Roemer, 1911) from the Late Bathonian of Europe (Westermann and Callomon 1988), novel traits distinguish it and is described here as a new species. Spath (1931) reported *K. aff. cosmopolitum* from his Macrocephalus Zone of Jumara, Kutch, which is represented by a complete microconch resembling closely the one of our present species, *K. spathi* <m> and has been synonymised with it. Kanjilal (1978) reported *Kheraicer probullatum* from Kutch which is now considered to be a variant of *Macrocephalites formosus* (Sowerby, 1840) (see Pandey and Westermann, 1988). *K. ex. gr. platystoma* reported by Bardhan and Datta (1987) from Jumara is now considered to be an extreme depressed variant of *K. cosmopolitum*. Krishna *et al.* (1987) il-

lustrated but did not describe a specimen as a microconch of *K. cosmopolitum* from the Golden Oolite of Keera. It appears, however, from the figure to be an adult macroconch of *K. bullatum* with a partially preserved body chamber. Bardhan *et al.* (1988) described *Bullatimorphites* sp. from Jumara which is in fact a *Kheraicer* species with a less depressed inner whorl and strong, coarse ribbing persisting on the adult body chamber. It has been redesignated here as *K. cf. hannoveranum* (see also Callomon, 1993; Jain *et al.*, 1996). Panday and Westermann (1988) reported a single specimen of *Bullatimorphites* (*Kheraicer*?) n. sp. A from the Middle (?) Bathonian of Patcham 'island', Kutch. It has peculiar *Bullatimorphites*-like inner whorls and a *Kheraicer*-like eccentrically coiled body chamber.

The spatio-temporal distribution of *Kheraicer* reveals its relatively narrow stratigraphic but wide biogeographic distributions. Yet little attention has been paid to its biostratigraphic potentialities except in Submediterranean France. In a previous attempt we have proposed a new biozonation scheme of the Upper Bathonian-Lower Callovian sequence of Kutch based on different stratigraphic ranges of *Kheraicer* and other important time-diagnostic taxa such as *Macrocephalites*, *Reineckeia* etc. (Bardhan *et al.*, 1999). An attempt has also been made for regional standard chronostratigraphy and interprovincial correlation.

Stratigraphy

Species of *Kheraicer* are distributed throughout the entire Callovian sequence of the basal Chari Formation in Kutch. One species straddles into the uppermost Batho-

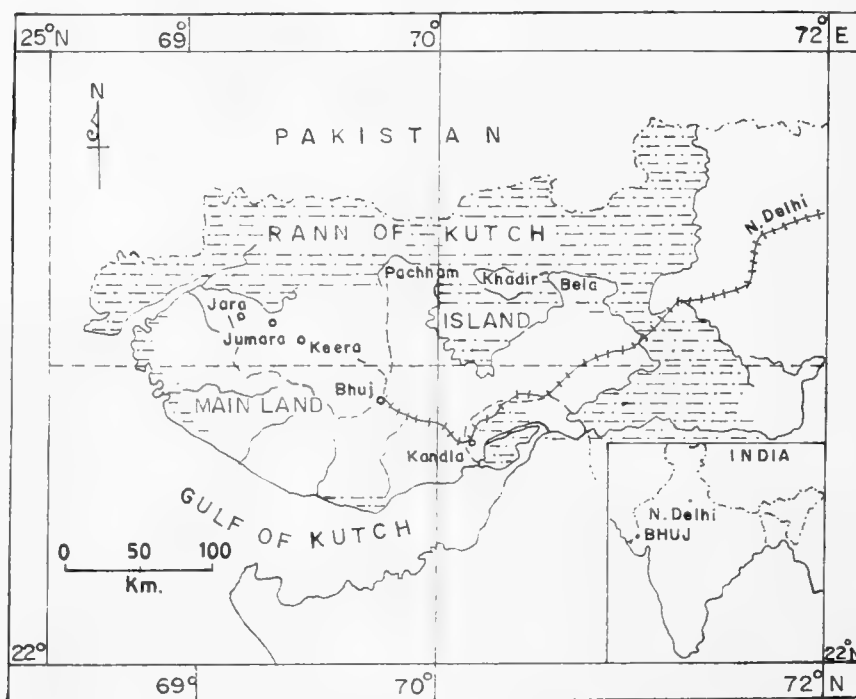


Figure 1. Geographic location of Kutch with Keera and Jumara, the type area of the Chari Formation. The patterned area is the Rann of Kutch.

nian bed in Jumara. The Chari Formation is a regionally persistent, highly fossiliferous unit and constitutes one of the four principal divisions of the Kutch Mesozoic (for details see Biswas, 1977; Mitra *et al.*, 1979; Krishna, 1984). It represents a near-continuous section ranging from the Upper Bathonian through the entire Callovian and Oxfordian. There are, however, reports of condensation of the se-

quence and time-averaging of fauna during the Oxfordian (Fürsich *et al.*, 1992; Halder and Bardhan, 1996). The Chari Formation represents a heterolithic facies consisting of shale, limestone and sandstone. The carbonate facies which yields the present *Kheraiceras* specimens is occasionally oolitic and is more dominant in the lower part of the sequence. The partially exposed, underlying Patcham Formation at Jumara is on the other hand predominantly calcareous, consisting of coral biostromes and limestone-marl alternations. Judging from the faunal associations and sedimentological evidence, these two formations are considered to be the product of a shallow-marine environment (Biswas, 1991; Datta, 1992; Fürsich and Oschmann, 1993).

The present *Kheraiceras* species have been systematically collected from different limestone beds of Jumara and Keera in the mainland of Kutch (Figure 1). Jumara is the stratotype of the Chari Formation and Keera is the type locality of *Kheraiceras cosmopolitum*. Stratigraphic occurrences of *Kheraiceras* species in the Jumara and Keera sections is shown in Figure 2.

All species of *Kheraiceras* described herein restrictedly occur within the zones spanning Upper Bathonian to Lower Callovian (Figure 3). Although these zones are based mainly on endemic Kutch ammonites, discoveries (e.g., Kayal and Bardhan, 1998) of some well time-diagnosed short-ranging taxa have made possible broad interprovincial correlation with other *Kheraiceras*-bearing provinces (for detailed discussion on age and correlation see Bardhan *et al.*, 1999).

Kheraiceras cf. hannoveranum is also known from

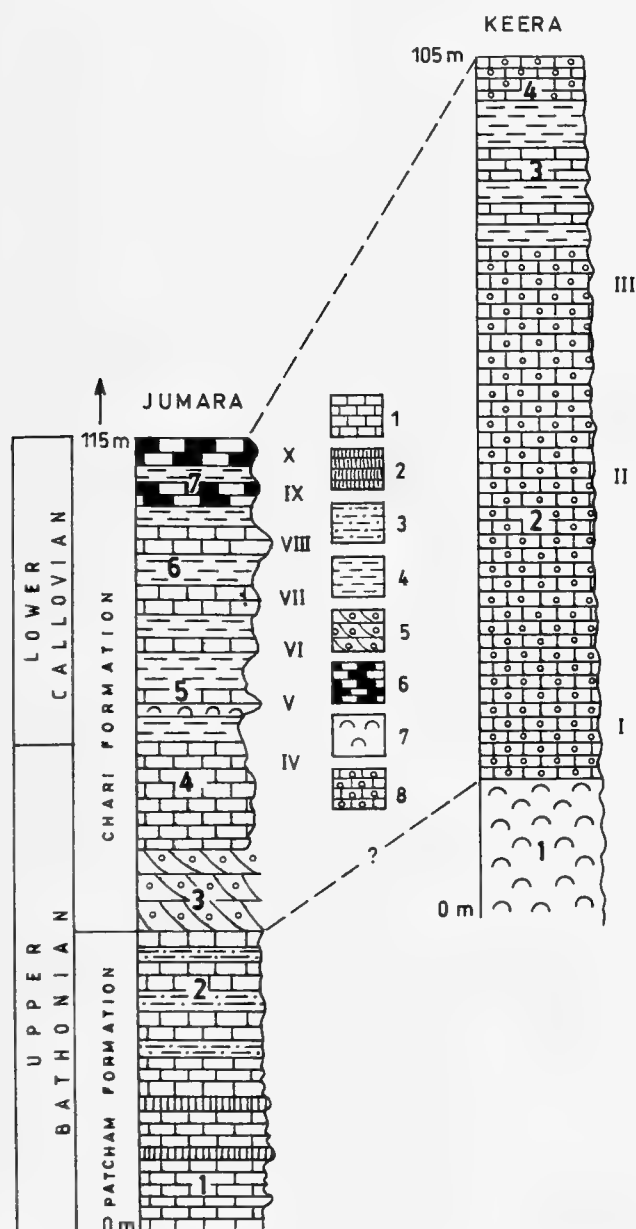


Figure 2. Stratigraphic sections at Jumara and Keera, Key. 1. white, cream or brown-coloured limestone; 2. coral biostrome; 3. marl; 4. shale; 5. cross-stratified, lenticular, green, oolitic limestone; 6. grey shelly limestone with thin alternating bands of red or white limestone and grey shale; 7. bioclastic grainstone; 8. oolitic limestone. Occurrences of different *Kheraiceras* species are indicated by horizon nos. (I–X).

| AGE | ZONE | SUBZONE | FAUNAL HORIZON | SPECIES |
|-----------------|-----------------|------------------|--------------------------------|--|
| EARLY CALLOVIAN | FORMOSUS | SEMILAEVIS | Nothocephalites semilaevis | K. sp.A. |
| | | | M. formosus | |
| | | FORMOSUS | Kamptokephalites lamellosus | |
| | | | Kampt. dimerus | |
| | | DIADEMATUS | K. bullatum | |
| | | | I. diadematus | |
| | | TRANSITORIUS | Kheraiceras cosmopolitum | |
| | | | I. transitorius | |
| | | MADAGASCARIENSIS | M. madagascariensis | |
| | | | Sivajiceras congener | |
| LATE BATHONIAN | CHRYSOOLITHICUS | CHRYSOOLITHICUS | Indocephalites chrysoolithicus | K. cosmopolitum K. bullatum K. cf. hannoveranum K. spathi |
| | | | Macrocephalites triangularis | |
| | TRIANGULARIS | HIANS | Procerites hians | |
| | | | | |

Figure 3. Range chart of different species of *Kheraiceras* in Kutch. Zones and Subzones are after Bardhan *et al.* (1999).

Baluchistan. Another new species described here, *Kheraicer* *noetlingi*, has been found only in Baluchistan. Both come from the Polyphemus Limestone, Mazardrik, Baluchistan.

Kheraicer

Faunal Associations

Kheraicer, though it ranges from Late Bathonian to Late Callovian (Hahn, 1969), is more diverse in Early Callovian, when other biostratigraphically important genera e.g., *Macrocephalites* Zittel and *Reineckeia* Bayle, also underwent adaptive radiation. In Submediterranean France *Kheraicer* is closely associated with reineckeids in the Lower Callovian beds, but macrocephalitids are rare (Cariou, 1984). In England, this part is marked by diverse macrocephalitid species but *Kheraicer* and reineckeids are absent (Callomon *et al.*, 1988). Kutch, on the other hand, includes ammonites of all these three groups and thus provides a unique opportunity for high resolution of biostratigraphic zonation and interprovincial chronostratigraphic correlation.

Recently Bardhan *et al.* (1999) proposed biostratigraphic zonations within the Bathonian-Callovian Stages of Kutch (Figure 3). The faunal horizons are not found in every section, but the subzones are regionally persistent and can be easily recognised for their characteristic ammonite assemblages in all the sections in the mainland of Kutch.

Kheraicer species are distributed throughout these assemblages except for the lowest one, i.e., the Triangularis Subzone. Different *Kheraicer* species have different

biostratigraphic ranges and like macrocephalitids, they are more diverse in the lowest Early Callovian. A brief summary of the faunal association of each *Kheraicer* species is given here (Figure 4). The relative abundance of other important ammonite species is discussed and a possible age correlation based on time-diagnostic or equivalent taxa is indicated.

The only *Kheraicer* species described from outside Kutch is *K. noetlingi* sp. nov. It comes from the Polyphemus Limestone, Mazardrik, Baluchistan (Noetling, 1896). It is associated with *Macrocephalites triangularis* 'group', *Clydonicer* *baluchistanense* (Spath) and *Choffatia* (*Homeoplanulites*) (Spath). This faunal association indicates a Late Bathonian age (see also Westermann and Callomon, 1988).

K. cf. hannoveranum first appeared in the Madagascariensis Subzone of the Chrysolithicus Zone in Kutch. It resembles the lectotype coming from the Upper Bathonian Orbis Zone of Germany. In the Madagascariensis Subzone, *Macrocephalites madagascariensis* is particularly abundant. It resembles *M. verus* (Buckman) in Europe which comes from the lowermost Callovian (Cariou, 1984; Callomon *et al.*, 1988). Another abundant macrocephalitid species is *Indocephalites chrysolithicus* (Spath). *Sivajicer* *congener* is also abundant while *Choffatia* sp. and *Oxycerites* (*Paroxycerites*?) sp. are less common. *K. cf. hannoveranum* also continues to the next assemblage, i.e., the Transitorius Subzone of the lowest Early Callovian where it co-occurs with diverse macrocephalitids, e.g., *Indocephalites transitorius*, *I. kheraensis*, *I. diadematus*, *Pleurocephalites elephantinus*, *Kamptokephalites lamellosus* and

| Ammonite association | Kheraiceras species | Other important ammonite species | | | | | | | | | | | | | | | | | | | | | | | |
|----------------------------------|--|----------------------------------|--------------------------|-----------------------------|---------------------------|-------------------------------|---------------------------|-------------------------------|-----------------------------|-----------------------------|--------------------------|----------------------------------|----------------------------|-------------------------|----------------------|------------------|-------------------------|------------------|-------------------|-----------------|----------------------|---------------------|---------------|----------------------|---------------------------------|
| | | Macrocephalites madagascariensis | Macrocephalites formosus | Indocephalites transitorius | Indocephalites kheraensis | Indocephalites chrysodithicus | Indocephalites diadematus | Pleurocephalites elephantinus | Dolkephalites subcompressus | Kamptokephalites lamellosus | Kamptokephalites dimerus | Kamptokephalites magnumbilicatus | Nothocephalites semilaevis | Nothocephalites asaphus | Eucydoceras eucyclum | Sukkosmalia opis | Reineckea tyranniformis | Reineckea anceps | Colokia oxyptycha | Choffatia cobra | Choffatia pardagatus | Choffatia recuperoi | Choffatia sp. | Sivallceras congener | Oxycerites (Paroxycerites?) sp. |
| Nothocephalites semilaevis | K. cosmopolitum | | ● | | ○ | ○ | × | × | ○ | ○ | ○ | × | ● | × | × | × | × | × | × | ○ | ○ | ● | | | |
| Macrocephalites formosus | K. cosmopolitum K. sp. A | | ● | | ● | ○ | ○ | ○ | ● | ● | ● | × | | | | | × | | | | | × | | | |
| Macrocephalites diadematus | K. cosmopolitum K. bullatum | | ○ | | ○ | ○ | ● | ● | ○ | ○ | ● | × | | | | | | | | | | × | × | | |
| Indocephalites transitorius | K. cosmopolitum K. bullatum, K. spathi K. cf. hannoveranum | | ○ | ● | ○ | ○ | ○ | ○ | ○ | ○ | ○ | | | | | | | | | | | | × | | |
| Macrocephalites madagascariensis | K. cf. hannoveranum | ● | | | | ● | | | | | | | | | | | | | | | | | × | ● | × |

● abundant, ○ common, x rare

Figure 4. Biostratigraphic distribution of *Kheraicer* species in Kutch in association with other important ammonites.

Dolikephalites subcompressus, *Macrocephalites formosus*. Besides, other *Kheraicer* species e.g., *K. cosmopolitum*, *K. bullatum*, *K. spathi* are also found from this level.

K. cosmopolitum is the most abundant species of *Kheraicer* and an endemic form. It has a longer stratigraphic distribution spanning the entire Formosus Zone of the Lower Callovian. This zone can be approximately correlated with the Lower Callovian *Macrocephalus* and *Gracilis* Zones of France (see also Krishna and Westermann, 1987; Bardhan *et al.*, 1999). It is more frequent in the Formosus Subzone, where it is associated with abundant *Macrocephalites formosus*, *Indocephalites kheraensis*, *Kamptokephalites dimerus*, *Kamptokephalites lammellosus*, *Dolikephalites subcompressus*, and rare *Choffatia recuperi*, *Reineckeia tyranniformis*. In the superjacent Semilaevis Subzone, *K. cosmopolitum* is associated with abundant *Nothocephalites semilaevis*, *Choffatia recuperi*. *Collotia oxyptica*, *Eucycloceras eucyclum*, *Subkossmatia opis* and *Nothocephalites asaphus* are rare at this level. Judging by this faunal association, the upper limit of *K. cosmopolitum* can reasonably be placed at the uppermost Early Callovian. *K. spathi* sp. nov. comes from the level immediately above the Bathonian-Callovian boundary. This horizon yields diverse *Kheraicer* species e.g., *K. cosmopolitum*, *K. cf. hannoveranum*, *K. bullatum*. The important macrocephalitids are *I. transitorius*, *I. chrysolithicus*, *I. diadematus*, *P. elephantinus* etc.

K. bullatum appeared slightly above the base of the Lower Callovian, spanning the upper part of the Transitorius and the entire Diadematus Subzones. Here it is associated with *K. cosmopolitum* and typical members of the faunal assemblage such as *I. diadematus*, *P. elephantinus*, *K. dimerus*, etc. This faunal association indicates a late appearance of *K. bullatum* in Kutch because it is already known from the Late Bathonian of Europe as well as South America (see Riccardi *et al.*, 1989; Sandoval *et al.*, 1990). We agree with Krishna and Cariou (1990) who correlated *K. bullatum*-bearing horizons of Kutch approximately with the upper Hervei Zone and Bullatus Zone of France on the basis of common associated taxa.

K. sp. A is represented by a single microconchiate specimen from the Formosus Subzone, which marks the disappearance of *K. bullatum*. It is associated with *K. cosmopolitum* and abundant *M. formosus*, *K. dimerus*, *K. lammellosus* and *D. subcompressus*.

Systematic Palaeontology

Superfamily Perisphinctaceae
Family Tuliitidae Buckman, 1921
Genus ***Kheraicer*** Spathi, 1924

Type species.—*Sphaeroceras cosmopolitum* Parona and Bonarelli 1895; original designation.

Kheraicer* *cosmopolitum
(Parona and Bonarelli, 1895)

Figures 5.1–5.4; 6c

Holotype.—GSI Type No. 2009. Internal mould with par-

tial shell remains, adult macroconch with last quarter of body chamber missing, from Golden Oolite of Keera.

Material.—In addition to the holotype, one macroconch (JUM/J/5) and two microconchs (JUM/J/2 and JUM/J/6) have been studied. All of them come from Jumara. The macroconch is an adult specimen with thin shell and last quarter of the body chamber missing, from Horizon V, Bed 5. The microconchs are almost complete, both coming from Bed 7; JUM/J/2 with terminal constriction present at flank and abraded on one side, from Horizon IX; JUM/J/6 with thin shell, from Horizon X.

Diagnosis.—Sphaeroconic, whorls extremely depressed and to a maximum in phragmocone, W/H ratio=2.8; body chamber occupies more than three-fourths of last whorl; beginning of body chamber marked by sudden whorl contraction and umbilical uncoiling following first a straight centrifugal line and then turning suddenly inwards; ribbing feeble in internal mould, disappears more rapidly near umbilicus than venter on body chamber, last seen at a diameter of 58 mm; umbilicus small, deep, umbilical wall gradually becomes steeper; flanks extremely short; septal suture with typically shallow tulitid U₂.

Description.—Detailed systematic description of macroconch, microconch, their synonymy and stratigraphic distribution have already been given in Bardhan *et al.* (1994).

Occurrence.—*Kheraicer* *cosmopolitum* is an endemic Kutch species. The holotype comes from the Golden Oolite (Bed 2), Keera. JUM/J/5 is collected from Horizon V, Bed 5, Jumara. JUM/J/2 and JUM/J/6 come from Horizon IX and X respectively of Bed 7, Jumara.

Kheraicer* *bullatum (d'Orbigny, 1846)

Figures 5.5a,b; 6a,b; 7.1–7.6; 8.1a–c; 9

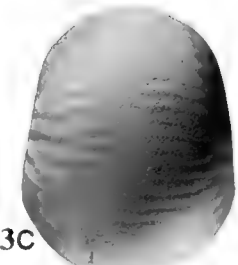
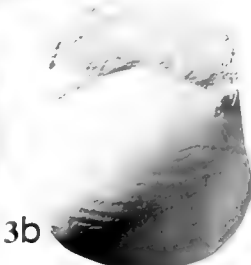
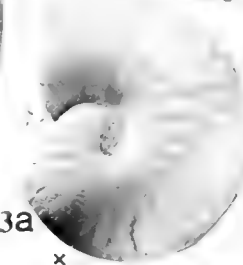
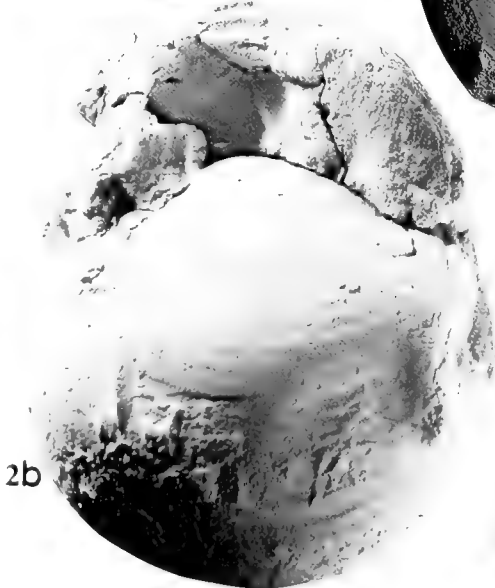
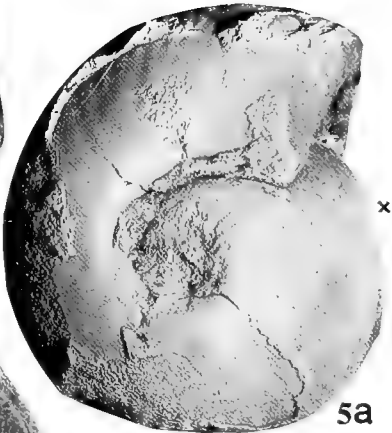
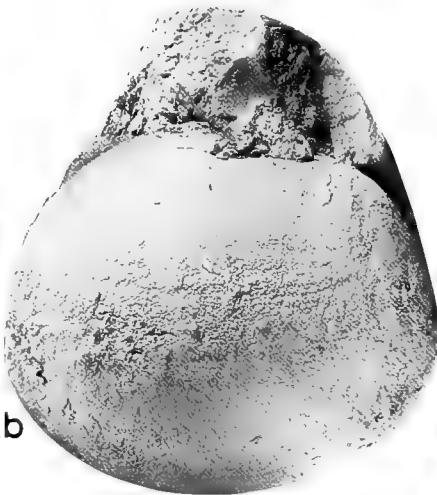
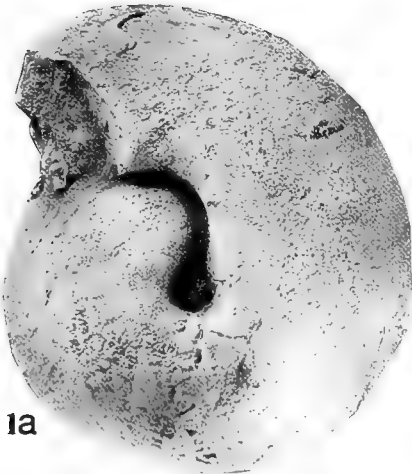
Macroconch.—

- 1846 *Ammonites bullatus* d'Orbigny, pl. 142, fig. 1, 2.
- 1954 *Bullatimorphites bullatus* (d'Orbigny). Arkell, text-fig. 34.
- 1958 *Kheraicer* *bullatus* (d'Orbigny). Westermann, pl. 22, fig. 1a–b.
- 1984 *Bullatimorphites (Kheraicer) bullatus* (d'Orbigny). Westermann, Corona and Carrasco, pl. 2, fig. 8a–b.
- 1987 *Kheraicer* *cosmopolita* Krishna, Cariou and Enay, p. 4, pl. 1, fig. 6.
- 1990 *Kheraicer* *bullatum* (d'Orbigny). Krishna and Cariou, p. 112.

Macroconch and microconch.—

- 1999 *Kheraicer* *bullatum* (d'Orbigny). Bardhan, Sardar and Jana, pl. 1, figs. 5–6.

Material.—Seven macroconch specimens, mostly adults, internal moulds with aperture missing. All come only from Bed 2, Keera; JUM/K/8–12, JUM/K/17 from lower horizon (Horizon I) and a near complete small variant, JUM/K/13, from upper level (Horizon II). Four microconchs with shell remains come only from Jumara; JUM/J/12 and JUM/J/13 with flared collar from Bed 6 (Horizon VII); JUM/J/14 with last quarter of body chamber missing, from Bed 5 (Horizon VI); JUM/J/11 near complete, abraded on one side, from basal part of Bed 7 (Horizon IX).



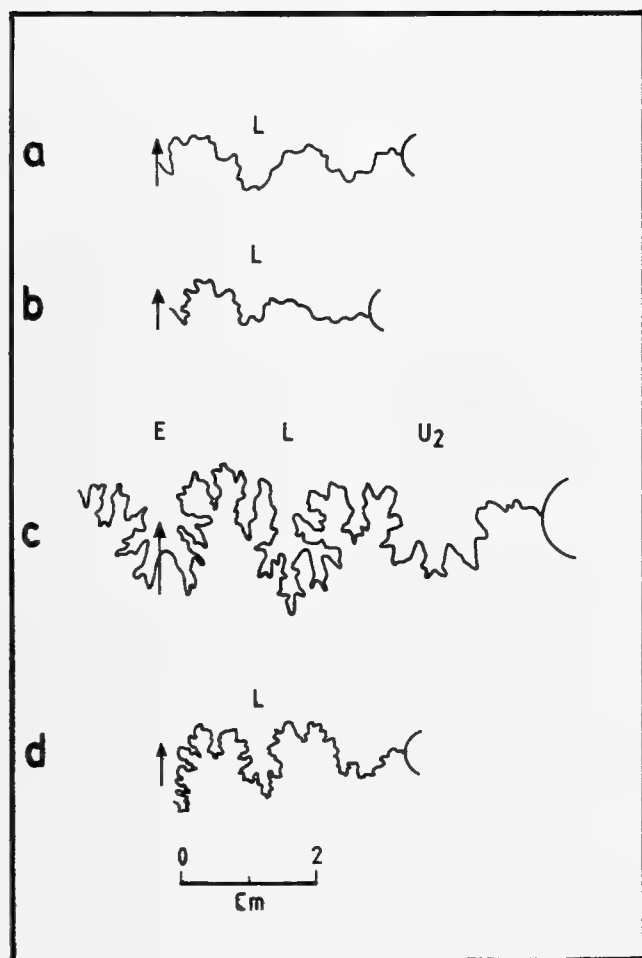


Figure 6. Septal sutures of *Kheraiceras*. **a, b.** Adult septal sutures of *Kheraiceras bullatum* (d'Orbigny) <M>, **a:** JUM/K/17 and **b:** JUM/K/9. **c.** Penultimate septal suture of the holotype (GSI type no. 2009) of *Kheraiceras cosmopolitum* (Parona and Bonarelli) <M>, after Spath 1928. **d.** Adult septal suture of *Kheraiceras* cf. *hannoveranum* (Roemer) <M>, JUM/J/10.

Measurements.—To record the remarkable modification of the adult body chamber, multiple measurements at different positions are given for a few specimens (Table 1).

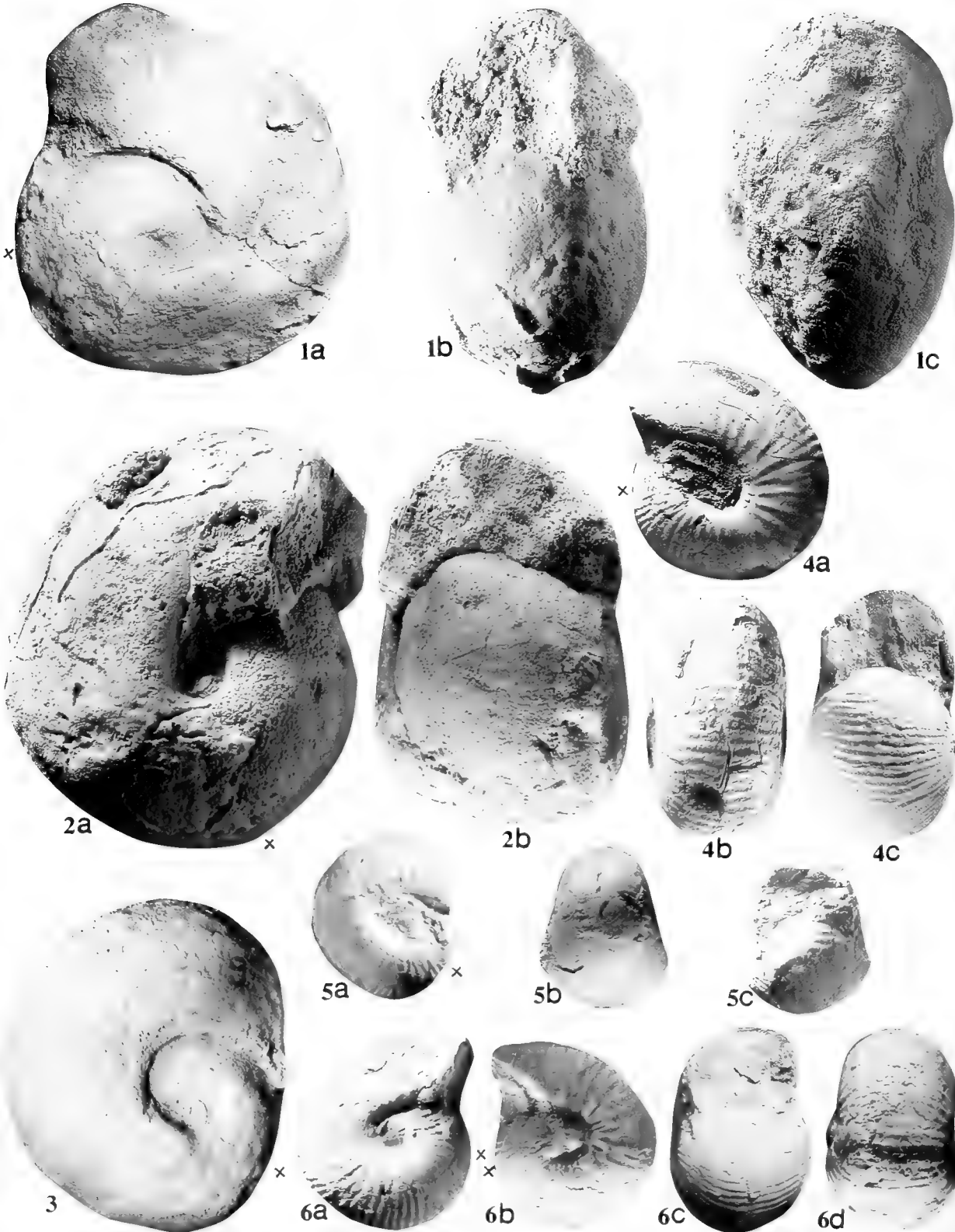
Description.—Macroconch<M>: Mostly internal mould, thin shell remains are rarely preserved. Body chamber

Table 1. Measurements for *Kheraiceras bullatum* (d'Orbigny, 1846) (in mm)

| Specimen | | D | U | H | W |
|--------------|-----------------|-----------------|--------|------|--------|
| Holotype | aperture | 78 | 31 | 25 | 40 |
| <M> JUM/K/8 | body chamber | 61 | 20 | 24 | 33 |
| | | 56(ca) | 13 | 26 | 32 |
| | | 52 | 8 | 28 | 38 |
| <M> JUM/K/9 | body chamber | 57 | 18 | 23 | 33 |
| | | 54 | 17 | 24 | 32 |
| <M> JUM/K/10 | end-phragmocone | 42(ca) | 9 | 26 | 36 |
| | body chamber | 59(ca) | 13 | 21 | 22 |
| <M> JUM/K/11 | body chamber | 49 | 11 | 24 | 28 |
| | | 57 | 20 | 22 | 23(ca) |
| <M> JUM/K/12 | end-phragmocone | 41 | 12 | 23 | 38(ca) |
| | aperture | 60 | 20 | 24 | 32 |
| <M> JUM/K/13 | end-phragmocone | 40 | 12 | 22 | 40 |
| | aperture | 47 | 14 | 18 | 27.5 |
| | body chamber | 43 | 10.5 | 19 | 26 |
| <M> JUM/K/17 | body chamber | 37 | 8 | 19 | 30 |
| | | end-phragmocone | 34(ca) | 8 | 14 |
| | | 34 | 8 | 14 | 23 |
| <M> JUM/J/11 | aperture | 67 | 20 | 29 | 38 |
| | end-phragmocone | 53(ca) | 12 | 28 | 42 |
| <M> JUM/J/12 | aperture | 41 | 11 | 14 | 19 |
| | body chamber | 34 | 10 | 16 | 21 |
| <M> JUM/J/13 | aperture | 43 | 14 | 15 | 23 |
| | body chamber | 36 | 10 | 15 | 21 |
| | body chamber | 34 | 9 | 16 | 21 |
| <M> JUM/J/14 | aperture | 35 | 12 | 16 | 20 |
| | body chamber | 30 | 7 | 13 | 19 |
| | body chamber | 29 | — | 14 | 19 |
| <M> JUM/J/14 | body chamber | 28 | 8 | 11 | 17 |
| | | 26 | 8 | 11.5 | 17 |
| | | 23 | 5 | 11.5 | 19 |

ellipticonic, phragmocone spindle-shaped. Early whorls involute, relatively depressed ($W/H=1.04-1.65$), one inflated variant (JUM/K/12) having $W/H=1.8$. Maximum diameter observed is 67 mm, the specimen (JUM/K/17, Figure 7-2a,b) was still larger as evident from the trace of the last quarter of body chamber. Body chamber occupying almost whole of the last whorl. It partially occludes umbilicus at diameter 41 mm–55 mm immediately after end-phragmocone stage and shows a strong deviation from regular spiral, where it becomes straight initially and then egresses out ec-

← **Figure 5.** Dimorphs of *Kheraiceras*. (All natural size). **1–4.** *Kheraiceras cosmopolitum* (Parona and Bonarelli). **1a, b.** Holotype <M> 2009, from Golden Oolite of Keera Bed 2, mostly internal mould, adult with incompletely preserved body chamber, highly depressed variant, lateral (a) and frontal (b) views. **2a–c.** Adult <M> with last quarter of body chamber missing, from Horizon V, Bed 5, Jumara, JUM/J/5, lateral (a), frontal (b) and ventral (c) views. **3a–c.** Almost complete <M>, from Horizon X, Bed 7, Jumara, JUM/J/6, lateral (a), frontal (b) and ventral (c) views. **4.** Adult <M>, body chamber fully preserved, but broken near venter, from Horizon IX, Bed 7, Jumara, JUM/J/2, note terminal constriction preserved at the flank, lateral view. **5a, b.** *Kheraiceras bullatum* (d'Orbigny), <M>, mostly internal mould with shell remains. Adult with almost completely preserved body chamber, from Horizon I, Bed 2, Keera, JUM/K/12, lateral (a) and frontal (b) views. x: base of body chamber.



centrically, resulting in a wider umbilicus near peristome. Umbilicus varies ontogenetically ($U/D=0.22-0.35$), holotype being more evolute ($U/D=0.40$) relatively narrow, shallow to moderately deep in inner whorls; umbilical margin distinct and wall steeper throughout adult body chamber. Flanks short to slightly wide, flat to gently curved with rounded ventrolateral margin. Venter rounded, broad. Adult phragmocone diameter ranges from 40 to 53 mm and even less in a small variant, where the figure is about 34 mm. Maximum width of shell attained just at beginning of adult body chamber. Width of body chamber contracts maximally at middle part from where it gradually increases again. Whorl height on the other hand gradually decreases with increasing shell diameter. Aperture missing. Whorl depressed, semicircular to semielliptical in apertural outline.

Ribbing not well discernible as shell is mostly internal mould. Ribs appear to be dense and fine on inner whorls, while broad, distant and restricted on venter and seen at least up to diameter 57 mm in the adult body chamber. The number of secondaries on first half of outer whorl is about 24.

Both lobes and saddles not deeply incised. Both external and lateral lobes are frilled, but former are more slender. Incipient internal lobes less frilled. External saddle weakly bifid, first lateral saddle shallow, broad (Figure 6-a, b).

Microconch <m>: Mostly shell remains, strongly resembles macroconch in many morphological features (Figure 9) except being smaller in size ($M : m=1.42$). Beginning of adult body chamber is marked by sudden egression of umbilical seam and maximum inflation ($W/H=1.25-1.65$) occurs just after it. Body chamber occupies nearly entire last whorl. Diameter of adult shell ranges from 35 to 43 mm. Apertural shape variable, elliptical to ovate. Peristome with slightly flared collar followed immediately by terminal constriction which cuts ribs obliquely. At middle part of body chamber of diameter 29 mm to 35 mm, apertural contraction is maximum, after which shell width again gradually increases towards aperture. Venter broad, strongly curved in inner whorls, becoming narrow and gently curved in body chamber. Laterals highly reduced, rounded up to end-phragmocone but widens and flattens later.

Both primary and secondary ribs are conspicuous, persistent up to peristome. Ribs fine and closely spaced in the early stage, becoming coarse and distant in outer whorl. Primaries rising from umbilical wall slightly rursiradiately, bifurcate irregularly at mid-flank or slightly higher. Secondaries and occasional solitaires go straight over venter. Number of secondaries in half whorl varies from 27 to 30.

Septal suture not discernible.

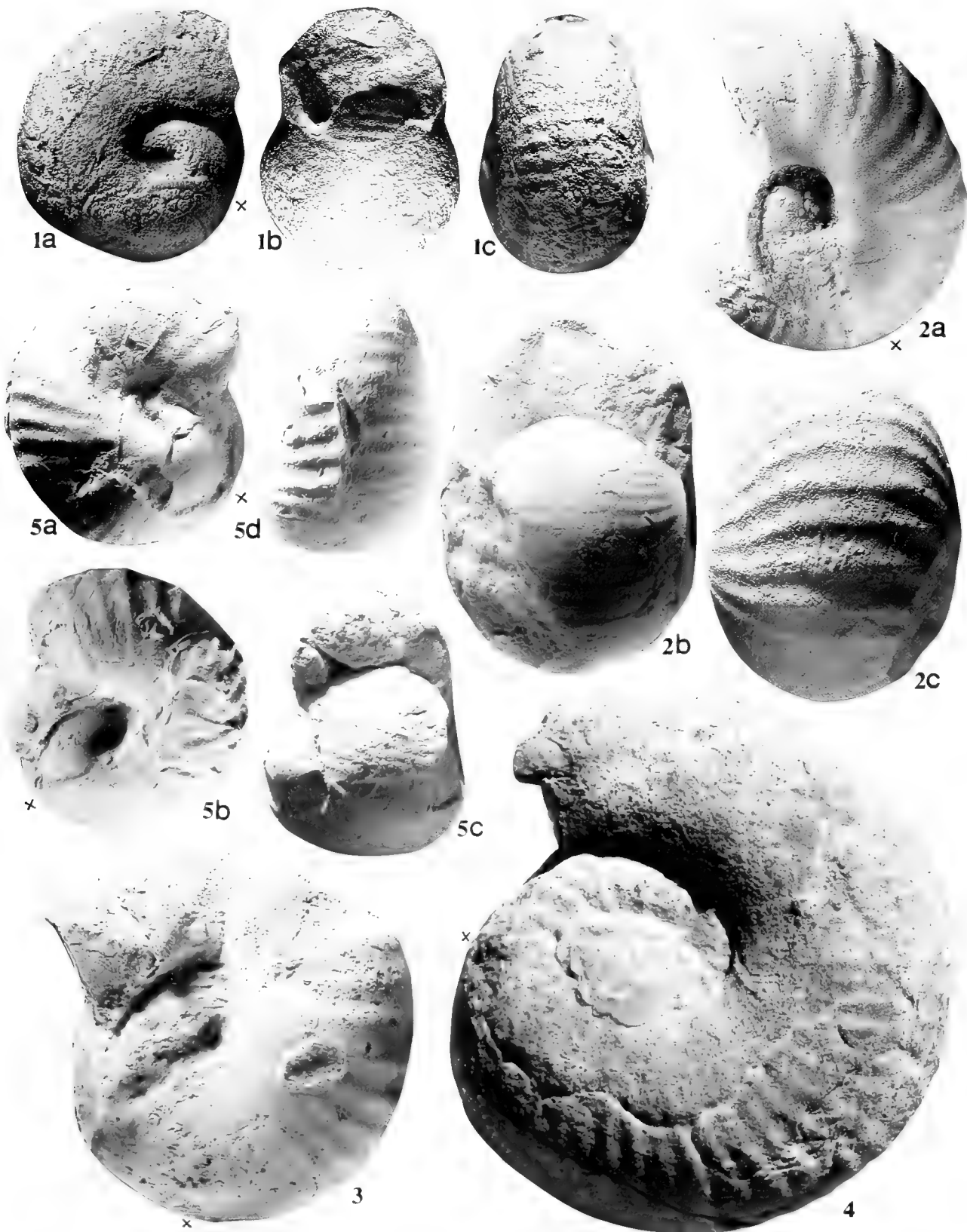
Discussion.—Macroconchs of the present form are closely

allied to the type specimens of *K. bullatum* (d'Orbigny, 1846) (see Arkell, 1954, text-fig. 34). They show strong resemblance in shell shape, whorl outline and nature of uncoiling of the umbilical seam. Ribbing pattern and the number of secondaries in the Kutch variant also agree more closely with the Lower Callovian *K. bullatum* s.s. The ribbing in the present macroconchs, however, is less conspicuous since most of them are internal moulds, and Arkell (1954) also pointed out that it is exaggerated in d'Orbigny's figure. However, d'Orbigny's species differs by its slightly larger adult shell diameter and relatively more inflated form. The stratigraphic and geographic distribution of *K. bullatum* is now better known. It is found in Europe, South America and Mexico, and ranges in age from Late Bathonian to Early Callovian (Cariou, 1984; Westermann *et al.*, 1984; Riccardi *et al.*, 1989; Sandoval *et al.*, 1990). The stratigraphic distribution of *K. bullatum* both in Kutch and France shows a phyletic size decrease (see also Krishna and Cariou, 1990). The relatively smaller adult size of the Kutch forms in comparison to those of Europe may, therefore, actually represent a smaller variant of a higher stratigraphic level or may be due to geographic variation (Bardhan *et al.*, 1999).

The microconch described here under the present species strongly resembles the macroconch of *K. bullatum* of both Kutch and European forms. Its phragmocone is similarly cadiconic but not much inflated like that of *K. cosmopolitum*, body whorl with typical *bullatum*-like uncoiling. The microconch, however, is characterised by much smaller adult size and apertural modification. In the microconch ribs are fine, dense, continuing all through the body whorl. Interestingly, in Kutch, although both dimorphs come from coeval stratigraphic horizons, they do not occur together. Macroconch specimens come from different stratigraphic levels within the Golden Oolite of Keera whereas the microconchs are found in different but coeval horizons of Jumara.

Microconch shows strong resemblance to different species of *Bomburites*. *B. devauxi* (de Grossouvre, 1891) (see Arkell, 1952, text-fig. 27), though similar in nature of shell shape and uncoiling, differs mainly by its smaller size, more depressed aperture and presence of strongly flared collar behind the terminal constriction. *B. globuliforme* (Gemmellaro, 1872) (see Arkell, 1952, text-fig. 27) has a shell size comparable to one of the variants of the present form (Figures 7-4a-c), but it is coarsely ornate and characterized by a peristome with a much flared collar. *K. prahecquense* of France also resembles the present form in shell diameter and *K. bullatum*-like other features. In Kutch both dimorphs are found at the same stratigraphic levels, but *K. prahecquense* appears only after the disappearance of *K.*

← **Figure 7.** *Kheraiceras bullatum* (d'Orbigny). (All natural size). **1a-c.** Adult <M>, internal mould, body chamber fully preserved, from Horizon I, Bed 2, Keera, JUM/K/8, lateral (a) frontal (b) and ventral (c) views. **2a, b.** Adult <M>, internal mould, almost completely preserved body chamber, from Horizon I, Bed 2, Keera, JUM/K/17, lateral (a) and frontal (b) views. **3.** Almost completely adult <M>, internal mould, aperture missing, from Horizon I, Bed 2, Keera, JUM/K/9, lateral view. **4a-c.** Adult <m>, with terminal constriction preserved near the flank, from Horizon VII, Bed 6, Jumara, JUM/J/12, lateral (a), ventral (b) and frontal (c) views. **5a-c.** Almost completely adult <m>, with partially preserved body chamber, from Horizon VI, Bed 5, Jumara, JUM/J/14, lateral (a), ventral (b) and frontal (c) views. **6a-d.** Complete adult specimen <m>, from Horizon VII, Bed 6, Jumara, JUM/J/13, lateral (a,b), frontal (c) and ventral (d) views. Note terminal constriction in 6b. x: base of body chamber.



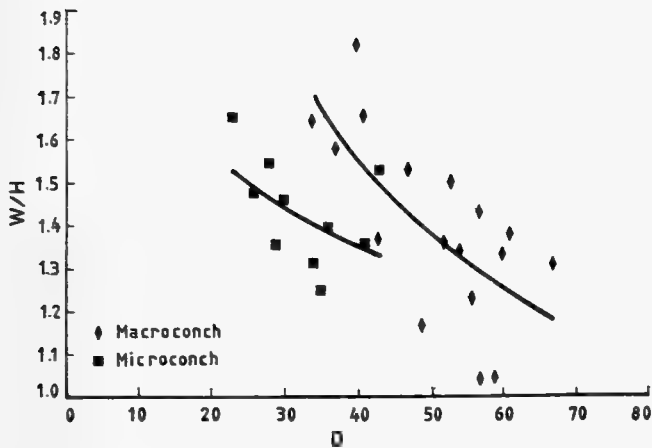


Figure 9. Best-fit growth curves of whorl section of macroconch and microconch of *Kheraiceras bullatum* (d'Orbigny).

bullatum, thus making two distinct subzones (Cariou, 1984). Recently, *Ammonites microstoma* d'Orbigny (see Arkell, 1954, text-fig. 35) has been considered as a possible microconch of *K. bullatum* (Westermann and Riccardi, 1979 and Westermann and Callomon, 1988). *A. microstoma*, though, with a less depressed phragmocone, has a gradual *Bullatimorphites*-like uncoiling of the body chamber. It appears that the present microconchiate forms are the better candidates to match to the true, i. e., macroconchiate form of *K. bullatum*.

The present macroconch closely resembles *K. cf. hannoveranum* <M>, described here, but the latter is larger and strongly ornate. Detailed comparison, however, is given in the discussion part of *K. cf. hannoveranum*.

Noetling's (1896) '*Sphaeroceras*' cf. *bullatum* is a giant *Kheraiceras* and considered as *K. cf. bullatum* by Pandey and Westermann (1988) and Westermann and Callomon (1988). Arkell (1954) also compared it with the European *K. bullatum* s.s. Noetling described the species from the Upper Bathonian Polyphemus Limestone, Baluchistan. We have inspected the only monotypic specimen reposit in the Geological Survey of India, Calcutta (Type No. 2915). Admittedly it is comparable with the European *K. bullatum* in coiling and ribbing pattern, but it is exceptionally large for the genus, having a diameter of 158 mm. Its body whorl is highly contracted and the aperture is barely in contact with the ventral surface of the preceding whorl. Besides, the

phragmocone does not become depressed as much as in *K. bullatum* and ribs disappear much earlier in the inner flank on the body chamber. The Baluchistan specimen is described here as a new species, *K. noetlingi* sp. nov.

K. cosmopolitum (Parona and Bonarelli, 1895), the type species, comes also from Kutch and stratigraphically overlaps the present species in the lower part of its range. This species and *K. bullatum* are closely related and their microconchs are also known. The nature of dimorphism is quite distinct and speaks for their specific separation. Both morphs of *K. cosmopolitum* have much inflated phragmocone, more depressed aperture and more eccentrically coiled body chamber than those of the present species. Microconchs of the two species are ornate to the end and characterised by apertural modification, but the microconch of *K. bullatum* has relatively fine, denser ribbing and more secondaries in the outer whorl than in *K. cosmopolitum*. Septal sutures are well discernible in macroconchs only, which are mainly represented by internal moulds. *K. cosmopolitum* has a more complex sutural pattern (Figure 6-c) at the same growth stage. Interestingly, both the species differ in macroconch-microconch size ratio which is greater in *K. cosmopolitum* ($M : m \approx 2.05$).

Kheraiceras spathi sp. nov. <m> described later, is readily distinguishable from the microconch of the present species by its elliptically coiled body chamber, less depressed and less evolute early whorls, and pronounced terminal constriction.

Microconch of the present species differs from *Kheraiceras* sp. A <m>, described later, in being larger with coarse ornamentation and widely spaced ribbing.

Westermann *et al.* (1984) described *B. (K.) bullatum* from Mexico based on a full-grown and almost complete specimen (pl. 2, fig. 8a-b). Its obsolete ribbing on the body chamber and number of secondaries agree closely with some of our specimens of the present species. However, this Mexican form is slightly larger and may be an older geographic variant since it comes from the Upper Bathonian horizon. *Bullatimorphites (Kheraiceras) v-costatus* from the Upper Bathonian of Caracoles, Chile is a large and coarsely ornate form (Riccardi *et al.*, 1989, pl. 8, figs. 3, 4). This form is even larger than true *K. bullatum* <M> (d'Orbigny, 1846) of Europe and the Kutch form. Its ribbing is strong, distant and seems to persist on most of the outer whorl, and thus perhaps agrees closely with contemporary *K. hannoveranum* (Roemer).

Recently Géczy and Galacz (1998) described a new Late Bathonian species *Bullatimorphites (Bullatimorphites) dietli* from South Hungary. The paratype of the species (Géczy

← Figure 8. Dimorphs of *Kheraiceras*. (All natural size). 1a-c. *Kheraiceras bullatum* (d'Orbigny) <M>, internal mould, small variant, complete adult specimen, from Horizon II, Bed 2, Keera, JUM/K/13, lateral (a), frontal (b) and ventral (c) views, note obsolete ribbing restricted on the venter. 2-5. *Kheraiceras cf. hannoveranum* (Roemer) <M> and <m>. 2a-c. Adult <M> with last 1/3 of the body chamber missing, from Horizon IV, Bed 4, Jumara, JUM P-2, lateral (a), frontal (b) and ventral (c) views. 3. Adult <M>, one half is damaged, last part of the body chamber crushed, from Horizon V, Bed 5, Jumara, JUM/J/10, lateral view. 4. Almost complete adult specimen <M>, one side damaged, from the Polyphemus Limestone, Mazardrik, Baluchistan, kept in Indian Museum, Calcutta, type no. H. 48.607, lateral view. 5a-d. Almost complete adult specimen <m>, peristome missing, from Horizon I, Bed 2, Keera, JUM/K/7, lateral (a,b), frontal (c) and ventral (d) views. Note retention of coarse, distant ribbing to the end. x: base of body chamber

and Galacz, 1988, pl. III, fig. 7) resembles our smaller, younger variant (Figure 8.1a–c) from the late Early Callovian in nature of umbilical uncoiling and adult body whorl length.

Sandoval *et al.* (1990) recently established dimorphism in *K. bullatum* from the Upper Bathonian of Mexico. They synonymised their microconch with *Bomburites microstoma*, but the Mexican form differs from that of d'Orbigny. It, in fact, is very closer to the present microconch and one Mexican variant (*ibid.* pl. 9, 3a–c) is barely distinguishable.

Occurrence. — *Kheraicerias bullatum* has a wide biogeographic distribution. Besides Kutch, it occurs in Europe, South America and Mexico from the Late Bathonian to Early Callovian. In Europe the species is abundant in France. The lectotype (see Arkell, 1954, text-fig. 34) comes from the Upper Bathonian. The species is common in the Bullatum Subzone of the Lower Callovian (Cariou, 1984). *K. cf. bullatum* is reported from the East Pacific faunal province. In Mexico it appears in the lower part of the Steinmanni Zone (=upper part of Restrocostatum Zone or Aspidoides Zone of Europe), and is associated with *Epistrenoceras histricoides*, indicating a Late Bathonian age (Westermann *et al.*, 1984; Sandoval *et al.*, 1990). In Argentina it comes from the Vergarensis Zone, which is equivalent to the Macrocephalus Zone of Submediterranean France (Riccardi *et al.*, 1989).

All seven macroconchs from Kutch localities come from different horizons within Bed 2, Keera. JUM/K/8–12, JUM/K/17 from Horizon I and JUM/K/13 from Horizon II. Four microconchs come from Jumara. JUM/J/14 from Horizon VI, Bed 5; JUM/J/12–13 from Horizon VII, Bed 6 and JUM/J/11 from Horizon IX, Bed 7.

Kheraicerias cf. hannoveranum (Roemer)

Figures 6d; 8.2–8.5

Macroconch.—

- 1911 *Sphaeroceras quenstedti* var. *hannoverana* n.v. Roemer, p. 42, pl. 7, figs. 16, 21, pl. 8, fig. 1.
 1915 *Sphaeroceras bullatum* d'Orbigny. Lóczy, p. 351, text-fig. 79.
 1925 *Kheraicerias ? stansfieldi* Spath, pl. I, fig. 2a–b.
 1952 *Bullatimorphites hannoveranus* (Roemer). Arkell, p. 108.
 1958 *Bullatimorphites bullatus hannoveranus* (Roemer). Westermann, p. 65, pl. 21, figs. a–b.
 1970 *Bullatimorphites* (*Bullatimorphites*) cf. *hannoveranus* (Roemer). Mangold, p. 303, figs. 96–97.
 1971 *Bullatimorphites cf. hannoveranus* (Roemer). Hahn, pl. 7, fig. 3.
 1988 *Bullatimorphites* sp. Bardhan, Datta, Khan and Bhaumik, pl. 1, fig. 1a–c.
 1993 *Kheraicerias* sp. nov. A. Callomon, p. 235.
 1994 *Bullatimorphites* (*Kheraicerias*) *hannoveranus* (Roemer). Dietl, p. 10, pl. 1, fig. 2.
 1997 *Bullatimorphites* (*Kheraicerias*) *hannoveranus* (Roemer). Mangold and Rioult, pl. 18, fig. 6.
 1998 *Bullatimorphites* (*Bullatimorphites*) *hannoveranus* (Roemer). Géczy and Galacz, pl. III, figs. 1a–b, 2a–b, text-fig. 9.

Macroconch and microconch.—

- 1999 *Kheraicerias cf. hannoveranus* (Roemer). Bardhan, Sardar and Jana, pl. 1, figs. 7–9.

Material. — The present collection includes three macroconchs and one microconch. Two macroconchs (JUM P-2, JUM/J/10) are collected from Beds 4 and 5 of Jumara (Horizons IV and V in Figure 2), Kutch, and the other one is from the Polyphemus Limestone, Mazardrik, Baluchistan, and now kept in the Indian Museum (H 48.607), Calcutta. The only microconch, JUM/K/7 comes from the lower part of the Golden Oolite (Bed 2, Horizon I in Figure 2) of Keera.

Measurements.—See Table 2.

Description.—Macroconch <M>: Shell ellipsoconic, moderately inflated, involute up to adult phragmocone stage and then becomes evolute with rapid uncoiling of umbilical seam. Whorl section depressed, ovate. Adult phragmocone diameter ranges from 45 to 60 mm. Adult body chamber covering more than 3/4 of the last whorl. Maximum shell diameter observed is about 100 mm. Maximum inflation (W/H=1.27–1.76) occurs at or just after end-phragmocone; both width and height show negative allometry afterwards.

Umbilicus shallow and umbilical margin is steep up to end-phragmocone diameter or early part of body chamber but later gradually becoming less inclined. Sudden egression of umbilical seam coincides with beginning of body chamber; first it goes straight up to about 18 mm length occluding partially umbilicus of inner whorl, then turns inwards eccentrically towards aperture resulting in a 'hook-shaped' body chamber. Flank short, barely existing in inner whorl but with ontogeny becomes broad and gently curved. Venter broad, highly curved at early stage but becomes gently rounded on adult body chamber. Ventrolateral margin is always rounded.

Shell coarsely ornate on body chamber. Phragmocone with relatively fine and dense secondaries; primaries short, regular and bifurcating on inner flank, and originating from umbilical margin. They disappear, resulting in smoothening of inner flank of body chamber while secondaries suddenly become coarse, distant and traced up to end of body chamber. Secondaries assume a broad, convex pattern aborally and then flex forward near ventrolateral margin and go over venter with slight forward projection. Number of secondaries on first half of outer whorl is 24.

Both external and lateral saddles are large, frilled.

Table 2. Measurements for *Kheraicerias cf. hannoveranus* (Roemer) (in mm).

| Specimen | D | U | H | W |
|-----------------------------|--------|----|--------|----|
| <M> JUM/J/10 body chamber | 72(ca) | 19 | 27 | 38 |
| | 61 | 20 | 34 | 44 |
| <M> JUM P-2 end-phragmocone | 51 | — | 26 | 40 |
| | 60 | 14 | 24 | 40 |
| <M> JUM P-2 body chamber | 49 | 7 | 25 | 44 |
| | 45 | 7 | 24 | 40 |
| <M> H 48.607 aperture | 99(ca) | 33 | 27(ca) | — |
| | 60(ca) | — | 24 | 34 |
| <m> JUM/K/7 aperture | 48 | 12 | 17 | 27 |
| | 42 | 13 | 22 | 28 |
| | 35(ca) | 5 | 23 | 33 |

External saddle bifid with deeply incised secondary lobes, lateral lobe deep, narrow (Figure 6-d).

Microconch <m>: It replicates macroconch in all major aspects barring size. Body chamber occupies almost whole of last whorl. Maximum diameter observed is 48 mm. Maximum inflation ($W/H \approx 1.59$) occurs on adult body chamber at diameter 35 mm followed by sudden contraction with decrease of both height and width. Aperture missing. Body chamber, initially after deviating from the regular spiral, goes straight for a distance of about 12 mm and then turns centrifugally towards the aperture.

Ornamentation similar to that on macroconch but both primaries and secondaries retained without losing strength up to end of preserved body chamber. Number of secondaries on first half of outer whorl is about 30.

Discussion.—The present species can be readily distinguished from other Kutch forms by its coarsely ornate ribbing which persists to the end of adult conch, sutural pattern and nature of dimorphism. However, it occupies morphometrically an intermediate position between highly depressed *K. cosmopolitum* and relatively compressed *K. bullatum* (see Figure 10).

The present species differs from *K. cosmopolitum* by its less contracted body chamber and less inflated phragmocone, relatively simple sutural pattern and more distant, coarse ribbing persistent up to the end of the body chamber. Moreover, in *K. cosmopolitum*, the growth of shell width relative to shell diameter shows negative allometry, while in the present species both width and height of the body chamber decrease with increasing shell diameter. Flanks are wider than in *K. cosmopolitum*. Moreover, dimorphic size ratio between these two species also differs.

The lectotype of *K. hannoveranum* from the Upper Bathonian Orbis Zone of Germany matches well with the macroconchs of the present species in having a less inflated phragmocone and coarse ribbing which persists to the end. Jain *et al.* (1996) also compared one of the variants (JUM P-

2, Figures 8-2a-c) of the present Kutch form with *Bullatimorphites* cf. *hannoveranus* (Roemer, 1911, pl. 8, fig. 1; Hahn, 1971, pl. 7, fig. 3) and *B. (Bullatimorphites)* cf. *hannoveranus* (Mangold, 1970, p. 303, figs. 96-97) from the Upper Bathonian Restrocostatum Zone of the Southern Jura. Callomon (1993) also noticed a similarity between the same Kutch specimen (JUM P-2) and *B. costatus* Arkell (Lissajous, 1923, p. 18, fig. 2), and *K. suivecum* (Roemer) (pl. 7, fig. 21). The latter species has now been regarded as a microconch of the present species (Géczy and Galacz, 1998) and the type specimens of *K. suivecum* (see Arkell, 1952, text-fig. 36) are quite comparable with the microconch of the present species (JUM/K/7) described herein (Figure 8-5a-d). All of them are characterised in having strongly ornate outer whorl and ribbing which continues to the end without losing strength.

The European macroconchs of the present species are larger in size and come from the older stratigraphic horizons. The present forms come from beds ranging in age from Late Bathonian to earliest Callovian. It appears that their smaller adult size may be due to geographic variation as well as younger stratigraphic age, since phyletic size decrease is found in many species of *Kheraiceras*.

The macroconch of the present species is a close ally of that of *K. bullatum*, but differs in relatively large adult size and less contracted and less aberrantly coiled body chamber. Besides, in *K. bullatum* ribs are finer, more numerous, restricted mainly on the venter, and disappear finally near the aperture, while coarse, distant ribs which persist throughout the last whorl characterise the present species. Remarkably, these differences are also observed in microconchs.

Kheraiceras? stansfieldi described by Spath (1925, pl. I, fig. 2a-b) from the 'Lower Callovian' Macrocephalus Zone of Madagascar, which is represented by an adult steinkern with crowded septal sutures and an incomplete body chamber, matches well with one of our specimens (Figures 8-2a-c) coming from the Madagascariensis Horizon. Both Kutch and Madagascan forms are similarly less depressed in apertural outline and have a rounded umbilical margin, and prorsiradiate ribs. Interestingly, the Madagascan form comes from the same locality and horizon which yield *Macrocephalites madagascariensis*. We believe that *Kheraiceras? stansfieldi* and the present *K. cf. hannoveranum* are conspecific.

Occurrence.—The lectotype of *K. hannoveranum* comes from the Upper Bathonian Orbis Zone of Germany. It closely resembles the Kutch form. The other Upper Bathonian specimens of the present species e.g., *Bullatimorphites* cf. *hannoveranus* (Roemer, 1911, pl. 8, fig. 1; Hahn, 1971, pl. 7, fig. 3), and *B. (Bullatimorphites)* cf. *hannoveranus* (Mangold, 1970, figs. 96-97, cited in Jain *et al.*, 1996) come from the Upper Bathonian Restrocostatum Zone of the Southern Jura.

Among our three macroconchs, JUM P-2 comes from Horizon IV, Bed 4, Jumara and JUM /J/10 from Horizon V, Bed 5, Jumara. The other one (H 48.607) comes from the Polyphemus Limestone, Mazardrik, Baluchistan. The only microconch (JUM/K/7) comes from Horizon I, Bed 2, Kerra.

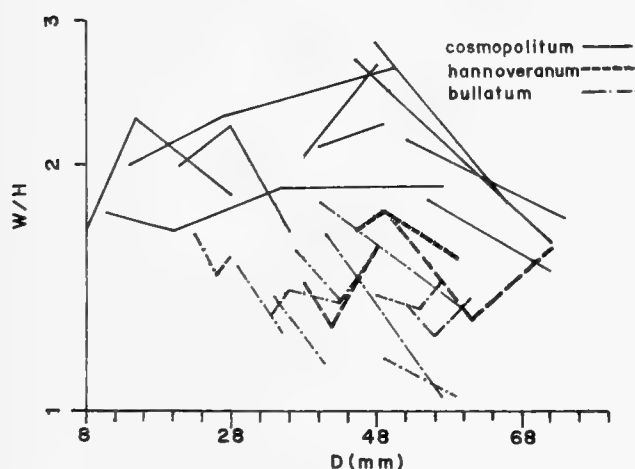
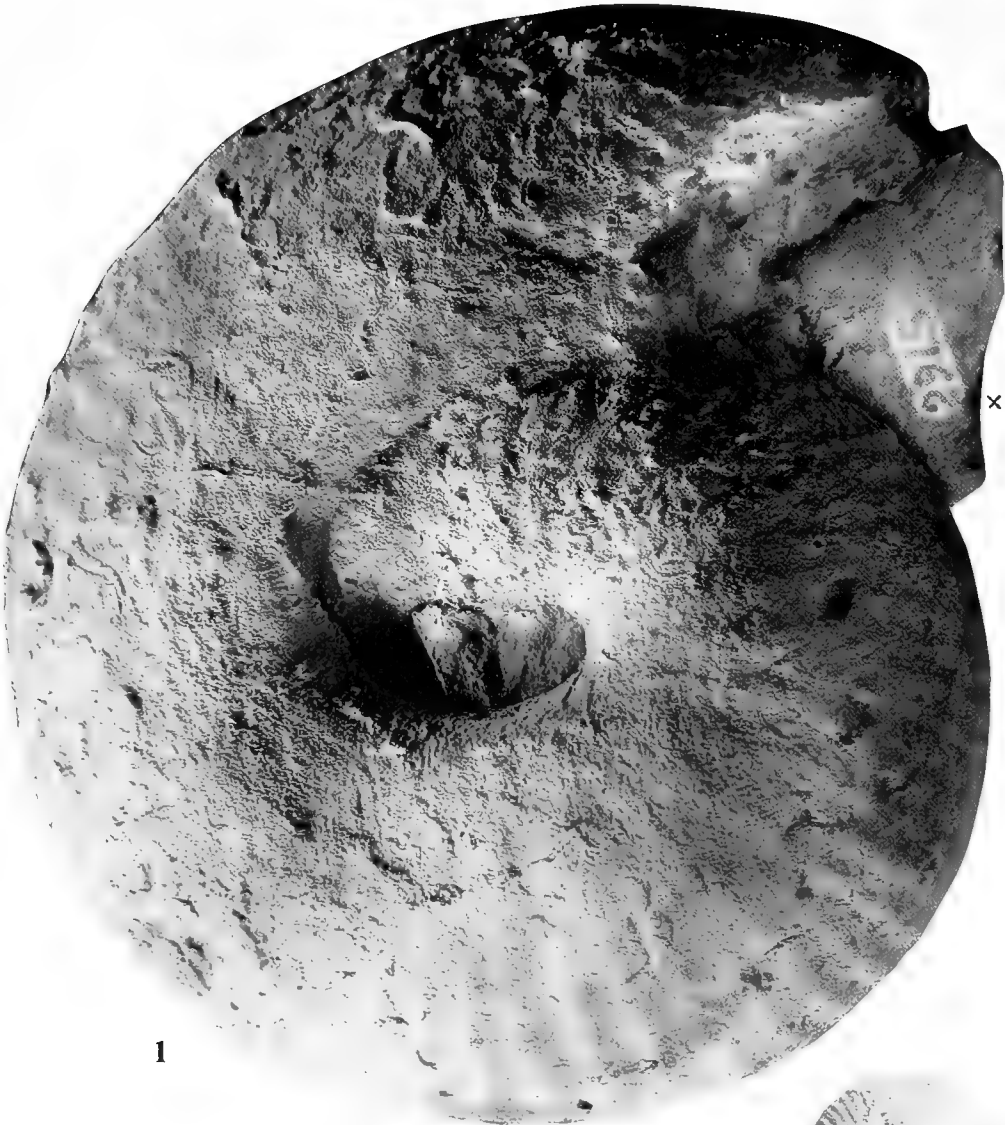
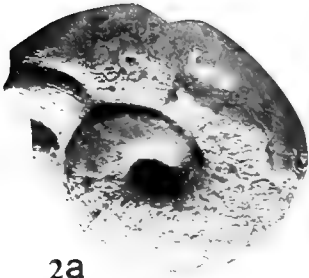


Figure 10. Growth curve of whorl section of both macroconch and microconch of three species of *Kheraiceras* in Kutch. Continuous line graph shows developmental change in a specimen.



1



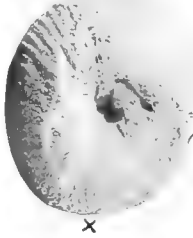
2a



2b



3b



3a



3c

***Kheraiceras spathi* sp. nov.**

Figures 11.2a, b

Microconch.—1931 *Kheraiceras* aff. *cosmopolita*, Spath, pl. XCVI, fig. 8a–b.1999 *Kheraiceras* sp. B. Bardhan, Sardar and Jana, pl. 1, fig. 12.

Material.—The present species is represented only by the holotype specimen (JUM/J/15) collected from Horizon V, Bed 5 of Jumara.

Diagnosis.—Shell small, compressed; inner whorls evolute, umbilical wall overhanging, depressed phragmocone, much contracted body chamber; width decreases during ontogeny, while height remains constant on outer whorl; retaining ancestral *Bullatimorphites*-like gradual uncoiling of body chamber, but characterised by flared peristome and highly contracted body chamber.

Etymology.—In honour of L.F. Spath, England, who first studied this species.

Measurements.—See Table 3.

Description.—Microconch <m>: Mostly internal mould, small, slender in shape ($W/D=0.84$ to 0.41 , during ontogeny of outer whorl). Inner whorl sphaeroconic, gradually uncoiled to elliptic outer whorl. Body chamber occupies almost whole of last whorl. Maximum diameter observed is 36 mm. Beginning of body chamber at about 22 mm, marked by slightly inward curving of outer whorl, thus occludes partially inner umbilicus ($U/D=0.21$) and followed thereafter by gradual eccentric coiling, so that at aperture body chamber is in contact only with ventral surface of preceding whorl ($U/D=0.33$). Inner whorl relatively evolute, depressed with laterals barely existing. Venter broad, strongly curved. Umbilical margin sharp, angular with overhanging umbilical wall. Inner flanks gradually flatten and umbilical margin becomes rounded near aperture. Maximum inflation ($W/H\approx 1.9$) of shell is attained after beginning of adult body chamber. Width decreases from the early part of adult body chamber with increase of shell size, but height remains almost unchanged. Laterals widen and venter narrows ontogenetically on body chamber; whorl section depressed, ovate (at aperture, $W/H=1.5$). Aperture with deep, broad terminal constriction which rises very sharply in rursiradial

manner near inner margin, then proceeds with a broad forward projection towards outer margin. Peristome projected forward at venter. Aperture immediately next to the constriction appears to be slightly flared in internal mould.

Ribbing fine, feeble on internal mould but appears to be persistent up to aperture. Suture not well discernible.

Discussion.—The microconchiate affinity of the present specimen is obvious in its smaller size and contracted adult body chamber with modifications at the peristome.

The present species strongly recalls '*Bomburites*', a genus which is now considered as microconchs of *Kheraiceras*. It is a close match of the holotype of the type species *Bomburites devauxi* (de Grossouvre, 1891) (Arkell, 1954, text-fig. 27). However, the present species differs mainly by its gradual uncoiling of the body chamber, fine ribbing, relatively larger adult size and absence of any prominent flared collar at peristome.

Spath's (1931) *Kheraiceras* aff. *cosmopolita* (pl. XCVI, figs. 8a–b) which comes from the same stratigraphic horizon (Bed 5) and same locality at Jumara, resembles so strikingly the present species that they appear to be conspecific.

The present species differs from microconchs of all other *Kheraiceras* spp. of Kutch by its compressed form, gradual uncoiling of umbilical seam and inwardly sloping umbilical wall. It differs from *K. bullatum* <m> by its gradual uncoiling of umbilical seam, elliptic body chamber and less ornate shell.

K. cosmopolitum <m> is the most tumid species ($W/D=0.69$ – 1.03) of the present group, with an eccentrically coiled body chamber. It has a more depressed phragmocone and aperture than those of *K. spathi*. Besides, ribs in *K. cosmopolitum* are coarser and more distant.

Microconch of *K. cf. hannoveranum* is readily distinguishable from the present form in having larger shell diameter, strong ornamentation, highly contracted and aberrantly uncoiled body chamber.

The original figure of *Ammonites microstoma* described by d'Orbigny (1846, pl. 142, figs. 3–4) which was refigured by Arkell (1954, text-fig. 35) is closely comparable with the present form, particularly with respect to gradual uncoiling of the body chamber and presence of a deep terminal constriction. *A. microstoma* d'Orbigny, 1846 is now considered as a microconch of *Kheraiceras*. It, however, differs from the present form in its larger size, strongly ornate shell and distinct collar.

Spath (1931) compared the present form with *K. globuliformi* (Gemmellaro, 1872) (Parona and Bonarelli, 1895, pl. VI, fig. 1) but the latter species is larger in size and characterized by coarse ribbing, more eccentrically coiled body chamber and highly flared peristome.

Occurrence.—The monotypic holotype (JUM/J/15) comes from a horizon (Horizon V, Bed 5, Jumara) which lies just

Table 3. Measurements for *Kheraiceras spathi* sp. nov. (in mm).

| Specimen | D | U | H | W |
|------------------------|----|----|----|------|
| <m> Holotype, aperture | 36 | 12 | 10 | 15 |
| JUM/J/15 body chamber | 29 | 8 | 10 | 17 |
| near end-phragmocone | 23 | 5 | 10 | 19.5 |

➦ **Figure 11.** Dimorphs in *Kheraiceras*. (All natural size). 1. *Kheraiceras noetlingi* sp. nov. <M>, holotype, (type no. 2915), complete adult, from the Polyphemus Limestone, Mazardrik, Baluchistan, now kept in Curatorial Division, Geological Survey of India, Calcutta, lateral view. 2a, b. *Kheraiceras spathi* sp. nov. <m>, holotype, internal mould, complete adult specimen with deep terminal constriction from Horizon V, Bed 5, Jumara, JUM/J/15, lateral (a) and frontal (b) views. 3a–c. *Kheraiceras* sp. A. <m>, adult with almost completely preserved body chamber, abraded near the last part, from Horizon III, Bed 2, Keera, JUM/K/16, lateral (a), frontal (b) and ventral (c) views; note fine, dense ribbing. x: base of body chamber.

above the Bathonian-Callovian boundary.

***Kheraiceras* sp. A**
Figures 11.3a–c

Microconch.—
1999 *Kheraiceras* sp. A. Bardhan, Sardar and Jana, pl. 1, fig. 11.

Material.—Only one specimen (JUM/K/16) collected from the Golden Oolite (Bed 2, Horizon III in Figure 2), Keera.
Measurements.—See Table 4.
Description.—Microconch <m>: Shell small, ellipsoconic?

Table 4. Measurements for *Kheraiceras* sp. A (in mm).

| Specimen | D | U | H | W |
|-----------------------|----|-------|------|----|
| <m> JUM/K/16 aperture | 23 | 7(ca) | 11.5 | 14 |
| body chamber | 31 | 7(ca) | 12 | 19 |
| | 26 | 4.5 | 11 | 20 |

(W/D≈0.46); strongly involute inner whorls. Adult phragmocone at about 21 mm. Maximum inflation (W/H=1.8) is attained after beginning of body chamber at 26 mm. Width of body whorl decreases rapidly with ontogeny while height

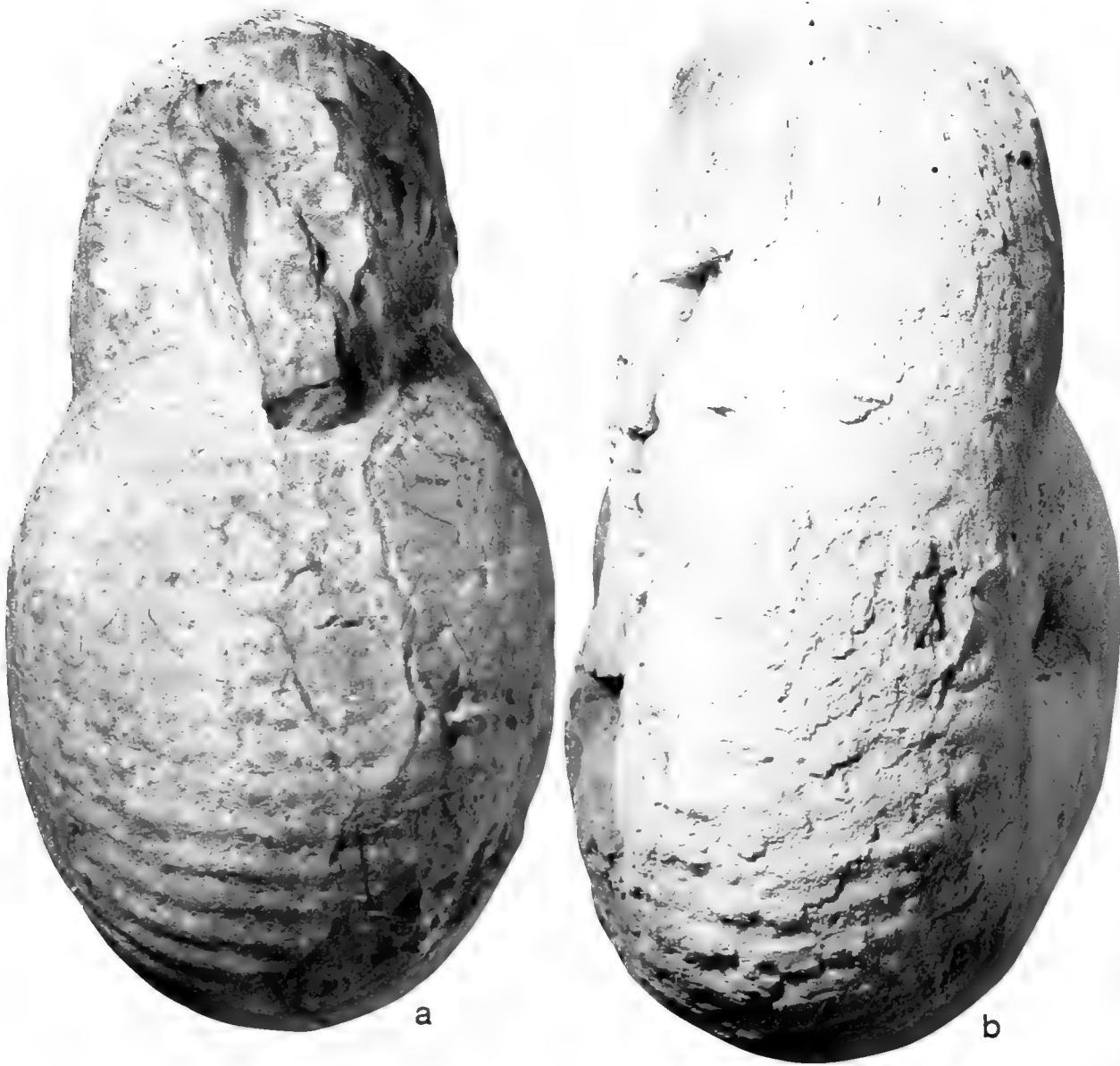


Figure 12. *Kheraiceras noettingi* sp. nov. <M>, same as figure 11.1, frontal (a) and ventral (b) views. (All natural size).

remains more or less same. Body chamber occupies more than 3/4 of last whorl, largest shell diameter being 31 mm, which occurs near middle part of body chamber. Afterwards shell diameter decreases slightly which may be due to secondary crushing of specimen. Aperture missing. Initially, umbilical seam deviates from regular spiral and goes straight in direction of largest shell diameter; then it suddenly turns inward and barely touches ventral surface of penultimate whorl. Venter broad, rounded and narrows down gradually towards aperture. Flanks short, less curved near mature phragmocone; both ventrolateral and umbilical margins gradual.

Ribs fine, dense, persisting till end. Primaries originating from umbilicus, straight to slightly rursiradiate near inner margin, and furcate irregularly either at or slightly above mid-flank. Secondaries feebly sinuous or straight across venter, about 34 on first half of outer whorl.

Septal suture not discernible.

Discussion.—The present species differs from *K. cosmopolitum* <m> by its smaller size, less depressed early whorls and more fine and dense ribbing.

It is smaller than *K. bullatum* <m> and body chamber is more contracted and aberrantly uncoiled. Besides, they differ in ribbing pattern and number of ribs per half whorl.

The described specimen also strongly recalls the holotype of '*Bullatimorphites*' *uhligi* (Popovichi-Hatzeg, 1905, pl. 6, fig. 7) (see Arkell, 1954, text-fig. 36). They both are characterised by fine dense ribbing and strongly involute phragmocone and may be conspecific if enough material is available. Unfortunately, the holotype of '*B. uhligi*' has an incomplete body chamber.

The unique holotype of *K. spathi* sp. nov. has a comparable adult shell diameter and fine, dense ribbing. It has, on the other hand, characteristic *Bullatimorphites*-like gradual uncoiling of body chamber and compressed shell shape. Besides, the present form differs also by its strongly involute inner whorls and less contracted aperture.

Occurrence.—Single specimen (JUM/K/16) from Horizon III of Bed 2, Keera.

Kheraiceras noetlingi sp. nov.

Figures 11.1 ; 12a, b

Macroconch.—

1896 '*Sphaeroceras*' cf. *bullatum* d'Orbigny, Noetling, pl. 6, fig. 2, 2a.

1933 *Kheraiceras quenstedti* (J. Roemer). Spath, p. 808.

1999 *Sphaeroceras bullatum* Bardhan, Sardar and Jana, pl. 1, fig. 10.

Material.—The holotype, a unique specimen described by Noetling (1896, pl. 6, fig. 2, 2a) from the Polyphemus Limestone, Mazar Drik, now repositied in GSI (Type No. 2915) and refigured here (Figures 11.1; 12a, b).

Diagnosis.—Unusually large for the genus; less cadiconic phragmocone, aperture highly contracted, inner whorls involute, body chamber eccentrically uncoiled and barely in contact with the ventral surface of the preceding whorl, apertural whorl section elliptical; ribbing coarse, distant, becoming obsolete in the first half of the body chamber.

Table 5. Measurements for *Kheraiceras noetlingi* sp. nov. (in mm).

| Specimen | | D | U | H | W |
|---------------|-----------------|-----|----|----|----|
| <M> Holotype, | aperture | 158 | 49 | 55 | 60 |
| GSI Type | body chamber | 132 | 34 | 51 | 60 |
| No.2915 | end-phragmocone | 127 | 17 | 50 | 90 |

Etymology.—In honour of F. Noetling, who first studied this species.

Measurements.—See Table 5.

Description.—Macroconch <M>: Internal mould, large, relatively compressed ($W/D \approx 0.7$). Complete adult specimen with maximum diameter 158 mm. Shell involute in early whorls, but becoming evolute in last whorl. Umbilical seam turns inward occluding partially umbilicus of inner whorls, end-phragmocone diameter 103 mm. Thereafter adult body chamber, which occupies more than 3/4 of last whorl, coils eccentrically and becomes very narrow at aperture, resulting in a wide umbilicus. Maximum inflation attained at end-phragmocone stage ($W/H=1.8$) followed by rapid contraction of body chamber which is maximum at about diameter 132 mm ($W/H=1.17$), thereafter height increases relative to width and at aperture $W/H=1.09$. In inner whorls, umbilical wall steep with umbilical margin relatively sharp to rounded but gradually becomes inclined with rounded umbilical margin on outer whorl. Flanks short and rounded in inner whorls, increase and tend to become less curved ontogenetically. Venter relatively broad and gently rounded up to end phragmocone, narrowing and arching strongly during later ontogeny. Apertural whorl section strongly depressed, ovate near beginning of body chamber and at aperture relatively compressed and elliptical.

Primary ribs prominent up to end phragmocone stage. They originate from umbilical wall slightly rursiradiately and furcate below midflank. Secondaries strong and distant, become gradually indistinct and restricted near venter and persist up to 3/4 of last whorl. Number of secondaries in first half whorl is about 30.

Discussion.—As far as we know the present species represents the largest *Kheraiceras* in the world. From its size alone it matches many *Bullatimorphites* species. *Bullatimorphites* and *Kheraiceras* form an evolving lineage and there exist several species which show morphologic overlapping (Sandoval, 1983; Pandey and Westermann, 1988). The affinity of the present species towards *Kheraiceras* is nevertheless unequivocal, based on its inflated phragmocone, eccentric coiling of umbilical seam and rapidly contracted body chamber. Although it comes from the Upper Bathonian sequence of Baluchistan (Noetling, 1896; Arkell, 1956), it is known that both *Bullatimorphites* and *Kheraiceras* overlap stratigraphically in the Upper Bathonian. *Bullatimorphites* has a very restricted geographic distribution and comes mainly from the Mediterranean Province.

Both Noetling (1896) and Arkell (1952) found the present holotype conspecific with the European *Kheraiceras bullatum* (d'Orbigny, 1846). Admittedly, the present species

resembles *K. bullatum* which ranges from the Late Bathonian to the earliest Callovian (Riccardi *et al.*, 1989), but the adult size difference between them is remarkable. Besides, d'Orbigny's type specimen of *K. bullatum* (see Arkell, 1952, text - fig. 34) has a more eccentrically coiled and less contracted adult body chamber and more depressed phragmocone. The present species also differs from the Indian form of *K. bullatum* <M>, described here, mainly by its adult size and coarser and distant ribbing.

Bullatimorphites cf. *hannoveranus* (Roemer, 1911) <M>, now known from both Europe and India, is also a larger form with coarser ornament and strongly recalls the present species. The present species, however, differs in having cadiconic, spindle-shaped inner whorls, highly contracted body chamber and less strong ribbing on the body whorl which becomes indistinct in the first half of body chamber and disappears thereafter. Study of *K. cf. hannoveranus* <M> reported here, makes the difference more apparent. Its body chamber is strongly ribbed and ribbing persists to the end without losing strength.

Occurrence. —The holotype comes from the Polyphemus Limestone bed, Mazardrik, Baluchistan. Judging from the faunal association which includes *Macrocephalites triangularis* 'group', *Clydoniceras baluchistanense* (Spath) and *Choffatia* (*Homeoplanulites*) (Spath), a Late Bathonian age of *K. noettingi* is certain (see also Westermann and Callomon, 1988).

Remarks

Kheraicerias is a stratigraphically important genus of near circum-global distribution. The genus evolved from *Bullatimorphites*, presumably during the Middle Bathonian. It underwent a speciation burst during the Late Bathonian to Early Callovian. After this peak, the genus declined and was reduced to a few stragglers by the Middle and Late Callovian (Hahn, 1969, 1971). Its early radiation was accompanied by a spectacular dispersion of *Kheraicerias* species to almost all biogeographic provinces. The Upper Bathonian of Europe yielded at least seven species including both micro- and macroconchs (Arkell, 1952). Among them, two important macroconchiate species, i.e., *K. hannoveranus* and *K. bullatum* had wide biogeographic distributions. *K. bullatum*, besides Europe, is also reported from Mexico (Westerman *et al.*, 1984; Sandoval *et al.*, 1990), South America (Riccardi *et al.*, 1989) and India (Bardhan *et al.*, 1999). *K. hannoveranus* on the other hand, is so far known to occur only in Europe and India. However, a specimen reported as '*Bullatimorphites* (*Kheraicerias*) *bullatus*' by Sandoval *et al.* (1990, pl. 9, fig. 4a-c) is known from South Mexico. It comes from the Upper Bathonian Steinmanni Zone. It has a marked similarity to the macroconch of Indian *K. cf. hannoveranus* (for details see Bardhan *et al.*, 1999). *Bullatimorphites* (*Kheraicerias*) *v-costatus* from the Upper Bathonian of Caracoles, Chile is a large and similarly coarsely ornate form (Riccardi *et al.* 1989, pl. 8, figs. 3, 4). It is larger in size than true *K. bullatum* <M> of Europe and Kutch. Its ribbing is strong, distant and seems to persist on the body chamber for a greater distance and thus agrees more closely with contemporary *K. hannoveranus* of

Europe.

Both *K. hannoveranus*, the putative ancestor, and the descendant *K. bullatum* continued to the Lower Callovian beds in Europe. While the former is restricted to the basal Lower Callovian horizon in Southern Germany and the Northern Jura (*Keplerites kepleri* horizon of Callomon *et al.*, 1988), *K. bullatum* proceeded further up to the *Cadoceras suevicum* fannal horizon of Subtethyan France (Cariou, 1984). Subsequently six new species of *Kheraicerias* appeared during the Early Callovian in these parts of Europe.

This paper describes six species of *Kheraicerias* of which three are new and four are endemic to Kutch and adjoining areas. Besides, Pandey and Westermann (1988) reported another Bathonian species of this genus from Kutch 'island'. The diversity falls in line with the Late Bathonian-Early Callovian radiation of the genus elsewhere, but a high degree of endemism may be attributed to the newly opened-up basin which was yet to establish well developed sea routes with other faunal provinces. Kutch was a pericratonic basin developed at the northwestern margin of the Indian plate with the beginning of fragmentation of Gondwanaland during the Bathonian (Biswas, 1991). The newly formed Kutch basin was immediately occupied by organisms which migrated from other areas and the basin acted as a cradle of evolution. The organisms that migrated here evolved rapidly to colonise the virgin ecospace (Halder, in press) and gave birth to a distinct faunal assemblage unique to India, Madagascar, East Africa and Baluchistan, all of which constitute what is known as the Indo-Madagascan or Ethiopian faunal province. Endemism and speciation events are all pervasive, affecting all major taxa. For example, corals showed a spectacular radiation; about seventy new species appeared in Kutch during Late Bathonian time (Gregory, 1900; Panday and Fürsich, 1993). Many new gastropods (Das *et al.*, 1999), brachiopods (Mukherjee *et al.*, in press) and nautiloids (Halder, in press) originated. Among ammonites, another circum-global genus, *Macrocephalites* Zittel, 1884, was also a product of Bathonian innovation and followed a course of spectacular Late Bathonian-Early Callovian radiation and migration (Datta *et al.*, 1996; Jain *et al.*, 1996). Kutch macrocephalitids are diverse and marked similarly by a high degree of endemism (Spath, 1927-33). However, in both cases, ecologically better adapted species spread to various faunal provinces in a fleeting manner (*sensu* Ager, 1984) and their first appearances seem to be isochronous everywhere. Such bioevents are of great value in intercontinental chronostratigraphic correlation and in establishing stage boundaries (Callomon, 1993).

The precise place of origin of *Kheraicerias* is unclear. The oldest species known until recently, *K. hannoveranus*, appears to be isochronous everywhere during the Late Bathonian. It is now generally believed that *Kheraicerias* evolved from *Bullatimorphites* through a complex heterochronic process involving neoteny (for details see Bardhan *et al.*, 1994). Evolutionary novelties were introduced, for example, sudden increase in degree of involution, inflation of phragmocone and occlusion of umbilicus by aberrantly-coiled, highly contracted body chamber, etc. (see also Westermann and Callomon, 1988). Two *Kheraicerias* species older than *K. hannoveranus* have been reported from

Kutch. The *Kheraicer* species from Baluchistan, *K. noetlingi*, is associated with some time-diagnostic ammonites indicating Late (? basal) Bathonian age (Westermann and Callomon, 1988). It is already a fully realised *Kheraicer* with the synapomorphies (sensu Eldredge and Cracraft, 1980) such as inflated phragmocone, occluded umbilicus, excentrically coiled and contracted body chamber without ribbing towards the aperture. *K. noetlingi* nonetheless still has a *Bullatimorphites*-like large adult size. Unfortunately little is known about its inner whorls. Interestingly, inner whorls are *Bullatimorphites*-like in another Kutch species, *Bullatimorphites* (? *Kheraicer*) sp. A described from the (?) Middle Bathonian by Pandey and Westermann (1988). It is a remarkable species showing a curious combination of many symplesiomorphies in the early whorls and advanced evolutionary features in the body chamber. If the age assignment is correct, it is the oldest *Kheraicer* known to date. Hence, in all probability, Kutch is a rare allopatric site (cf. Gould and Eldredge, 1977) where an immigrant ancestor, *Bullatimorphites*, gave rise to *Kheraicer*. The newly emerged Kutch basin subsequently prompted speciation and migrational events when sea - routes became well established.

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SHORT NOTES

Replacement names for Permian stauraxon radiolarians

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Abstract. New names are proposed for two genera of Permian stauraxon radiolarians to correct existing homonymy; the replacement names are *Raciditor* Sugiyama for *Nazarovella* De Wever and Caridroit and *Kimagior* Sugiyama for *Deflandrella* De Wever and Caridroit. This action makes the family Deflandrellidae De Wever and Caridroit invalid according to Art. 39 of ICZN (1999), therefore the family Kimagioridae is established to replace Deflandrellidae.

Key words: *Deflandrella*, *Nazarovella*, replacement name, Permian, stauraxon radiolarians

Introduction

Radiolarians are diverse marine zooplankton having a long evolutionary history beginning, to our knowledge, with the Cambrian period (e.g., Won and Below, 1999). When discussing the evolution, phylogenetic classification and systematics of the Radiolaria of a particular period or era (e.g. Permian, Mesozoic), it is essential to establish a geological-historical context by examining materials of the preceding and subsequent geologic ages. This approach to research will ensure correct knowledge of the characteristics of each period or era.

However, most radiolarian researchers tend to specialize throughout their careers in the radiolarians of a particular geologic age. For example, those working on Paleozoic radiolarians generally do not have a basic knowledge of Cenozoic radiolarians. At the least, when we establish new taxa, it is necessary to consult a variety of monographic studies on radiolarians of other geologic time periods to avoid taxonomic confusion created by the creation of homonyms and synonyms.

In this short paper, I introduce new names for two genera of Permian stauraxon radiolarians which are junior homonyms. The invalid names were originally in honor of famous radiolarian researchers. When creating such names, particular attention should be paid to the likely possibility of the names already having been employed by other researchers.

Systematic paleontology

Superfamily Ruzencevispongacea Kozur, 1980

Remarks.—Some researchers have used the name Latentifistulidea Nazarov and Ormiston, 1983, for this superfamily (e.g. Nazarov and Ormiston, 1983; Sashida and Tonishi, 1986). However, this is obviously an invalid name

according to Art. 36 of ICZN (1999), as mentioned in detail by Kozur and Mostler (1989).

Family Ormistonellidae De Wever and Caridroit, 1984
Genus *Raciditor* Sugiyama, new name

Not *Nazarovella* Kozur and Mostler, 1979, p. 68 (type species: *N. tetrafurcata* Kozur and Mostler, 1979).

Nazarovella De Wever and Caridroit, 1984, p. 101 (type species: *N. gracilis* De Wever and Caridroit, 1984).

Type species.—*Raciditor gracilis* (De Wever and Caridroit) = *Nazarovella gracilis* De Wever and Caridroit, 1984.

Remarks.—The generic name *Nazarovella* was first used by Kozur and Mostler (1979) for Triassic spherical radiolarians (spumellarian or entactinarian) possessing isometrically arranged spines with a quadrifurcated tip. Based on Arts. 23 and 60 of ICZN (1999), therefore, the replacement name *Raciditor* is given herein for *Nazarovella* proposed by De Wever and Caridroit (1984), who studied Permian stauraxon spumellarians from the Ultra-Tamba terrane of SW Japan, and named those stauraxon spumellarians having one short horn and three, long and grooved arms forming a flattened-tetrahedral structure as *Nazarovella*.

Etymology.—Named by use of an anagram of the family name of Dr. M. Caridroit, who first made excellent studies on the Ultra-Tamba terrane, SW Japan, using radiolarians. This name is of masculine gender.

Family Kimagioridae Sugiyama, new name

Deflandrellidae De Wever and Caridroit, 1984.

Type genus.—*Kimagior* Sugiyama, described below as a new name for *Deflandrella* De Wever and Caridroit, 1984.

Remarks.—Since the type genus of the family Deflandrellidae De Wever and Caridroit, 1984, is a junior homonym as discussed below, a replacement name for the

family is called for based on Art. 39 of ICZN (1999).

Genus *Kimagior* Sugiyama, new name

Not *Deflandrella* Loeblich and Tappan, 1961, p. 227 (type species: *Campylacantha cladophora* Jørgensen, 1905).

Deflandrella De Wever and Caridroit, 1984, p. 99 (type species: *D. manica* De Wever and Caridroit, 1984).

Type species. — *Kimagior manicus* (Dewever and Caridroit) = *Deflandrella manica* De Wever and Caridroit, 1984.

Remarks.—Since the generic name *Campylacantha* had already been used, Loeblich and Tappan (1961) introduced a replacement name *Deflandrella* for a homonymous name, *Campylacantha* Jørgensen, 1905, which was established for a plagiacanthid nassellarian from Norwegian plankton materials. Some radiolarian researchers have regarded *Deflandrella* Loeblich and Tappan as a junior subjective synonym of *Neosemantis* Popofsky, 1913 (e.g. Goll, 1979), whereas others have treated *Deflandrella* and *Neosemantis* as independent genera (e.g. Petrushevskaya, 1981). In any event, *Deflandrella* proposed by Loeblich and Tappan (1961) still remains valid taxonomically, which means that the identical name *Deflandrella* used by De Wever and Caridroit (1984) for Permian stauraxon spumellarian with three coplanar tubes is invalid.

Etymology.—Named by creating an anagram of a local place name, Kamigori, Hyogo Prefecture, SW Japan, near the type locality of the type species. This name is of masculine gender.

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行 事 予 定

- ◎第150回例会は、2001年1月27日(土)と28日(日)に「茨城県自然博物館」で開催されます。27日にシンポジウム「新生代軟体動物古生物学の最近の動向(世話人:野田浩司・天野和孝・島本昌憲・間嶋隆一)」が行われます。個人講演の申し込み締切日は2000年12月1日(金)です。
- ◎2001年年会・総会は、2001年6月29日(金)、6月30日(土)、7月1日(日)に「国立オリンピック記念青少年総合センター」で開催されます。21世紀最初の年会ですので、「21世紀の古生物学」を統一テーマとし、29日に統一シンポジウム、30日と1日に17件の課題別シンポジウムが行われる予定です。現在、学会の「将来計画委員会」によってプログラムの詳細を立案中です。一般講演はポスター講演だけに限って受け付けます。口答発表形式による一般講演はありませんのでご注意ください。ポスター講演の申し込み締切日は2001年5月9日(水)です。
- ◎第151回例会(2002年1月下旬開催予定)の開催申し込みは、今のところありません。
- ◎2002年年会・総会(2002年6月下旬開催予定)には福井県立博物館から開催申し込みがありました。
- ◎古生物学会では、小人数で実施されるワークショップやショートコースを主催しております。学会から金銭を含む援助を行なうことができますので、企画をお持ちの方は行事係までお問い合わせ下さい。

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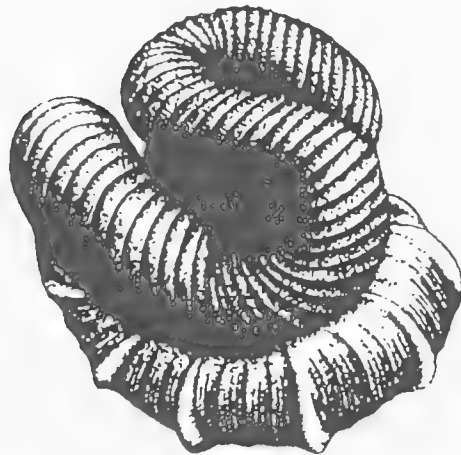
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Cover: Idealized sketch of *Nipponites mirabilis* Yabe, a Late Cretaceous (Turonian) nautiloid ammonite. Various reconstructions of the mode of life of this species have been proposed, because of its curiously meandering shell form (after T. Okamoto, 1988).

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***Gyronautilus*, a new genus of Triassic Nautilida from South Primorye, Russia**

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Abstract. A new genus of Triassic Nautilida, *Gyronautilus*, is proposed for material from the Lower Triassic of South Primorye, Russia. The new genus differs from previous known genera of the family Grypoceratidae by its gyroconic shell with subrectangular whorl sections and a near-marginal siphuncle. A new subfamily, *Gyronautilinae*, within the Grypoceratidae is also proposed.

Key words: Early Triassic, *Gyronautilus*, Nautilida, Olenekian, South Primorye

Introduction

The Triassic deposits in South Primorye, Far East of Russia, yield well-preserved nautilids, some of which species have been described by previous authors (Diener, 1895; Kiparisova, 1954, 1961; Zakharov, 1978). *Syringoceras praevolutum* was proposed by Kiparisova (1961) on the basis of a single small specimen collected by N.K. Trifonov in 1948 from the Lower Triassic of the Abrek Bay area, about 45 km southeast of Vladivostok. The exact locality and horizon of the specimen were not described, but recently we found a large and complete specimen identified as *S. praevolutum* from the type locality (Figure 1). In this paper we describe the early to adult features of the species, and propose a new subfamily and genus based on the specimen.

The specimen utilized herein is deposited in the National Science Museum, Tokyo (NSM).

Note on Stratigraphy

The Lower Triassic strata exposed along the eastern coast of Abrek Bay are lithostratigraphically divided into two formations, the Lazurnaya Bay and Zhitkov Formations in upward sequence, as defined by Zakharov (1996, 1997) along the shore of Lazurnaya (= Shamara) Bay and the east coast of Russian Island near Vladivostok.

The Lazurnaya Bay Formation unconformably overlies the Permian Abrek Formation and consists of basal conglomerate and gray, fine-grained, bedded sandstone with lenses of coquinooid calcareous sandstone. Its thickness is 57.9 m in the section surveyed. It contains the ammonoids *Gyronites*

subdharmaus Kiparisova and *Koninckites?* sp., the brachiopod *Lingula* sp., the bivalves *Promyalina vetusta* Bencke and *Eumorphotis multiformis* (Bittner) in the middle part, and the cephalopods *Hedenstroemia* sp., *Meekoceras boreale* Diener, *M. subcristatum* Kiparisova, *Ambites* sp. indet., and *Gyronautilus praevolutum* (Kiparisova), as well as the brachiopods *Abrekia sulcata* Dagys and *Lingula borealis* Bittner in the upper part (Zakharov and Popov, 1999). These fossils suggest the Upper Induan in the middle part and the Lower Olenekian (lower part of the *Hedenstroemia bosphorensis* Zone) in the upper part of the formation. The Induan/Olenekian boundary is located at 55 m above the base of the formation.

The overlying Zhitkov Formation consists mainly of dark grey siltstone with calcareous nodules and intercalations of fine-grained sandstone. The formation is more than 87.3 m thick in the section studied. The ammonoids *Inyoites spicini* Zakharov, *Parahedenstroemia conspicienda* Zakharov, *Prosphingitoides magnumbilicatus* (Kiparisova), *Dieneroceras* sp., *Meekoceras boreale* Diener, *M. subcristatum* Kiparisova, *Koninckites* aff. *timorensis* Wanner, *K. varaha* (Diener), *Arctoceras septentrionale* (Diener), and *Flemingites* sp., as well as the bivalves *Phaedrysomocheilus* sp. and *Promyalina putiatinensis* (Kiparisova) were found in the lower part of the formation, suggesting an early Olenekian age (upper part of the *Hedenstroemia bosphorensis* Zone).

Paleontological description

Order Nautilida Agassiz, 1847
Superfamily Trigonocerataceae Hyatt, 1884
Family Grypoceratidae Hyatt in Zittel, 1900

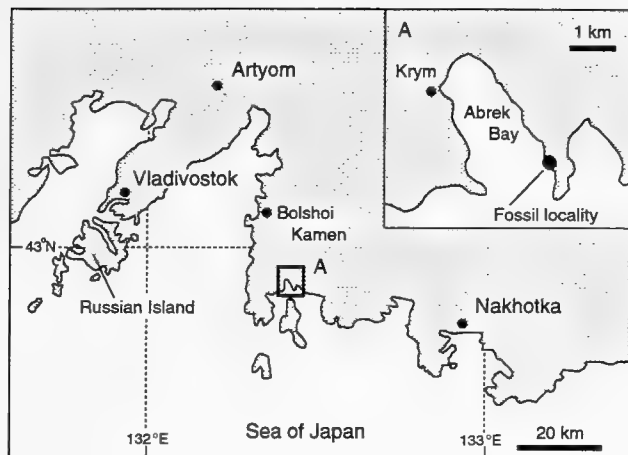


Figure 1. Map showing the fossil locality in South Primorye, Far East Russia.

Subfamily Gyronautilinae, subf. nov.

Diagnosis.—Gyroconic shell with flattened venter. Suture with distinct ventral and lateral lobes.

Composition.—One genus: *Gyronautilus* Zakharov and Shigeta.

Remarks.—Kiparisova (1961) described "*Syringoceras*" *praevolutum* in 1961 from the Lower Triassic of South Primorye and included it in the family Syringonautilidae. Shimansky (1962) recognized four subfamilies in the family Grypoceratidae: Domatoceratinae, Grypoceratinae, Syringonautilinae and Clymenonautilinae. During our investigation of Kiparisova's species we experienced problems with determination of its subfamily assignment, and concluded that it seems to be a representative of a new, previously unknown subfamily of the family Grypoceratidae. However, the nomenclatural and taxonomic history around the type genus of Grypoceratidae, *Grypoceras* Hyatt, 1883 is very complicated (T. Engeser, 2000, personal communication) and was not completely correctly investigated by Engeser and Reitner (1992).

Distribution.—Lower Triassic in South Primorye, Russia.

Genus *Gyronautilus*, gen. nov.

Type species.—*Gyronautilus praevolutum* (Kiparisova).

Diagnosis.—Gyroconic shell with subrectangular whorl-sections and a near-marginal siphuncle. Suture with shallow ventral lobe, broad lateral lobe, and deep dorsal lobe.

Discussion.—The new genus is discussed with *Gyronautilus praevolutum*.

Geological distribution.—Lower Olenekian.

Gyronautilus praevolutum (Kiparisova, 1961)

Figures 2–4

Syringoceras praevolutum Kiparisova, 1961, p.25, pl.4, fig. 2.

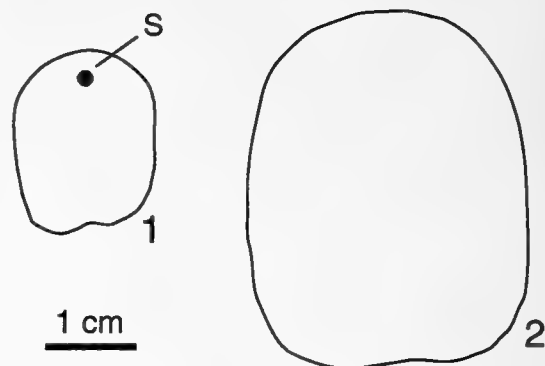


Figure 2. Whorl cross sections of *Gyronautilus praevolutum* (Kiparisova), NSM PM16132, at whorl height of 18.0 mm (1) and 39.3 mm (2). S: siphuncle.



Figure 3. Suture line of *Gyronautilus praevolutum* (Kiparisova), NSM PM16132, at whorl height of 25 mm.

Holotype.—CGM 12/5504 figured by Kiparisova (1961, pl.4, fig.2) from the Lower Triassic (Olenekian?) of Abrek Bay in South Primorye, Russia.

Material.—One specimen, NSM PM16132.

Description.—Shell moderately large, reaching 92.6 mm in diameter, rapidly expanding gyroconic conch, consisting of 1.7 whorls. Embryonic shell 18.2 mm long, exogastrically curved, consisting of 0.4 whorl, attaining 7.4 mm height and 7.0 mm width at nepionic constriction. First whorl subquadrate in cross section, with near-marginal siphuncle, attaining 18.1 mm height and 14.7 mm width: umbilical opening 8.2–13.4 mm across. Adult whorl subrectangular in cross-section with rounded-inflated venter, well-rounded shoulder and concave dorsal side, with near-marginal siphuncle, attaining 39.7 mm height and 36.1 mm width at last septum. Body chamber partly preserved, attaining 45.2 mm height and 36.6 mm width at adoral end. Shell surface not preserved. Suture consisting of shallow ventral lobe, broad lateral lobe, and deep dorsal lobe.

Discussion.—Kiparisova described the only previously known middle stage of *Gyronautilus praevolutum* on the basis of a fragment of the phragmocone reaching 17.0 mm height and 15.0 mm width at the last septum. The specimen described herein is a large and nearly complete one from the embryonic shell to a part of the adult body chamber. Characteristic features described by Kiparisova (1961) are also observed in the middle stage of specimen NSM PM16132.

Gyronautilus praevolutum is placed within the family Grypoceratidae because of its flattened venter and suture with ventral and lateral lobes. Among the previously de-

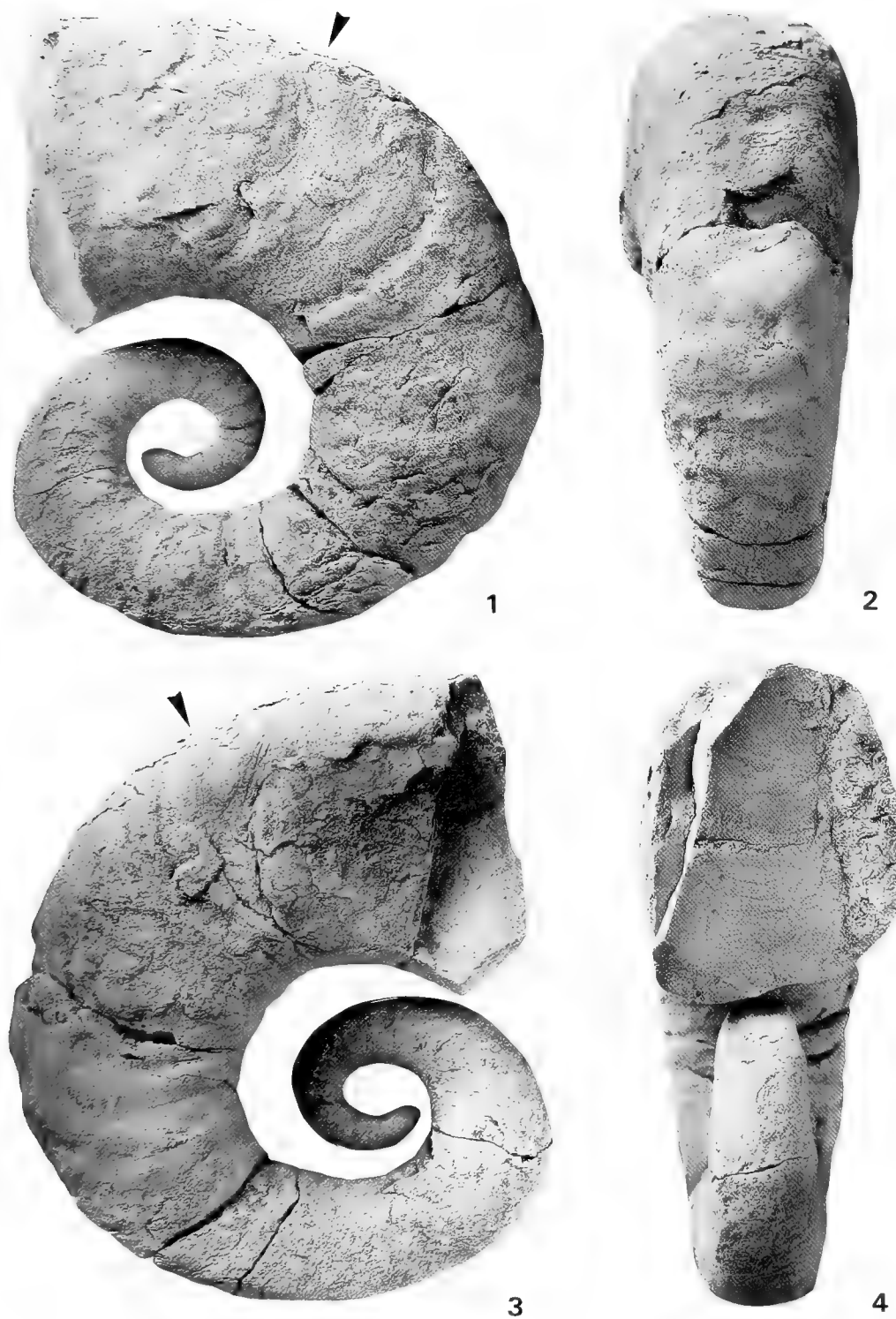


Figure 4. *Gyronautilus praevolutum* (Kiparisova), NSM PM16132. Right lateral (1), back (2), left lateral (3) and frontal (4) views, $\times 1.0$. Arrow marks indicate the position of the preserved last septum.

scribed genera of the family, the shape of the conch and the suture of *Gyronautilus* show closest affinities with the Permian *Domatoceras*. The sutures of both are similar, with rounded ventral and lateral lobes (Kummel, 1964). *Gyronautilus* shows some affinities to Triassic *Grypoceras* and *Menuthionautilus*, but the latter two differ in the proportions of sutural elements, in general forms of the conch, and in the siphuncle position (Kummel, 1953, 1964). It seems best to consider that *Gyronautilinae* is an offshoot of *Domatoceratinae*.

Occurrence.—NSM PM16132 was collected from the uppermost part of the Lazurnaya Bay Formation in the Abrek Bay area, *Hedenstroemia bosphorenses* Zone of the Lower Olenekian.

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Discovery of Early Cretaceous (Barremian) decapod Crustacea from the Arida Formation of Wakayama Prefecture, Japan

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Abstract. *Hoploparia* sp. (Astacidea, Nephropidae) and *Callianassa* (s. l.) *sakakuraorum* sp. nov. (Thalassinidea, Callianassidae) are described from the Lower Cretaceous Arida Formation in Wakayama Prefecture, Japan. Both genera are recognized for the first time from Lower Cretaceous (Barremian) deposits of Japan. These occurrences indicate that *Hoploparia* and *Callianassa* reached Japan—the west side of the North Pacific region—by the Barremian.

Key words: Arida Formation, Cretaceous, Crustacea, Decapoda, Japan

Introduction

Early Cretaceous decapod Crustacea from Japan previously were only known from the Aptian Miyako Group, northwestern Japan (Takeda and Fujiyama, 1983). The purpose of this paper is to describe two species of decapods, *Hoploparia* sp. (Astacidea, Nephropidae) and *Callianassa* (s. l.) *sakakuraorum* sp. nov. (Thalassinidea, Callianassidae) from the Lower Cretaceous Arida Formation of Wakayama Prefecture, southwestern Japan. Hitherto, *Hoploparia* from the Lower Cretaceous of the North Pacific region has been known from the Hauterivian of Oregon (Feldmann, 1974), while *Callianassa* (s. l.) has not been found in Lower Cretaceous deposits of that region.

The specimens were collected from sandy mudstone exposed at Suhara [Loc. 02 of Komatsu (1999)], Yuasa-cho, Wakayama Prefecture. Obata and Ogawa (1976) and Matsukawa and Obata (1993) indicated that the geologic age of the formation is Barremian. Komatsu (1999) studied the depositional environments and molluscan assemblages of the Arida Formation in the area and divided the formation into four depositional facies. The decapod fossils occurred in his facies 3, which is characterized by the predominant occurrence of *Nanonavis yokoyamai* and seems to indicate an inner-shelf paleoenvironment (Komatsu, 1999).

The described specimens are deposited in the Mizunami Fossil Museum (MFM).

Systematic paleontology

Infraorder Astacidea Latreille, 1802
Superfamily Nephropoidea Dana, 1852
Family Nephropidae Dana, 1852
Subfamily Homarinae Huxley, 1879
Genus *Hoploparia* McCoy, 1849

Hoploparia sp.

Figure 1.1, 1.2

Description. — *Hoploparia* with small-sized body. Carapace laterally compressed. Anterior half of carapace poorly preserved. Rostrum lacking. Surface finely granulated. Postcervical groove deep dorsally, obliquely extending ventrally. Hepatic groove obscurely defined, curving to join antennal and cervical grooves. Cervical groove deep, slightly arcuate, extending ventrally to join antennal groove. Antennal groove nearly straight. Gastro-orbital groove shallow, extending to near upper part of cervical groove. Antennal region with antennal ridge. Dorsal and supraorbital ridges well developed. Intermediate carina weakly developed. Branchial region finely punctuate.

Abdominal somites 1–6 smooth. Pleuron of somite 1 somewhat reduced; posteroventral corner with posteroventrally directed spine. Pleuron of somite 2 subrectangular; anteroventral corner rounded; ventral margin gently convex; posteroventral corner with posteroventrally directed spine; posterior margin gently concave; surface with marginal furrows joining transverse furrow on anterior part of tergum. Pleura of somites 3 and 4 with sharp, posteroventral corners; surfaces with shallow, broad marginal furrow along posterior margin. Pleuron of somite 6 reduced. Telson, uropod and pereopods unknown.

Discussion. — The carapace with dorsal, supraorbital and antennal ridges readily distinguishes the species from two known Japanese species, *Hoploparia miyamotoi* Karasawa, 1998 from the Maastrichtian Izumi Group and *Hoploparia kamuy* Karasawa and Hayakawa, 2000 from the Turonian-Santonian part of the Upper Yezo Group. *Hoploparia* sp. possesses characters most like those of *Hoploparia collignoni* (Van Straelen, 1949) from the Albian of Madagascar and *Hoploparia riddlensis* Feldmann, 1974

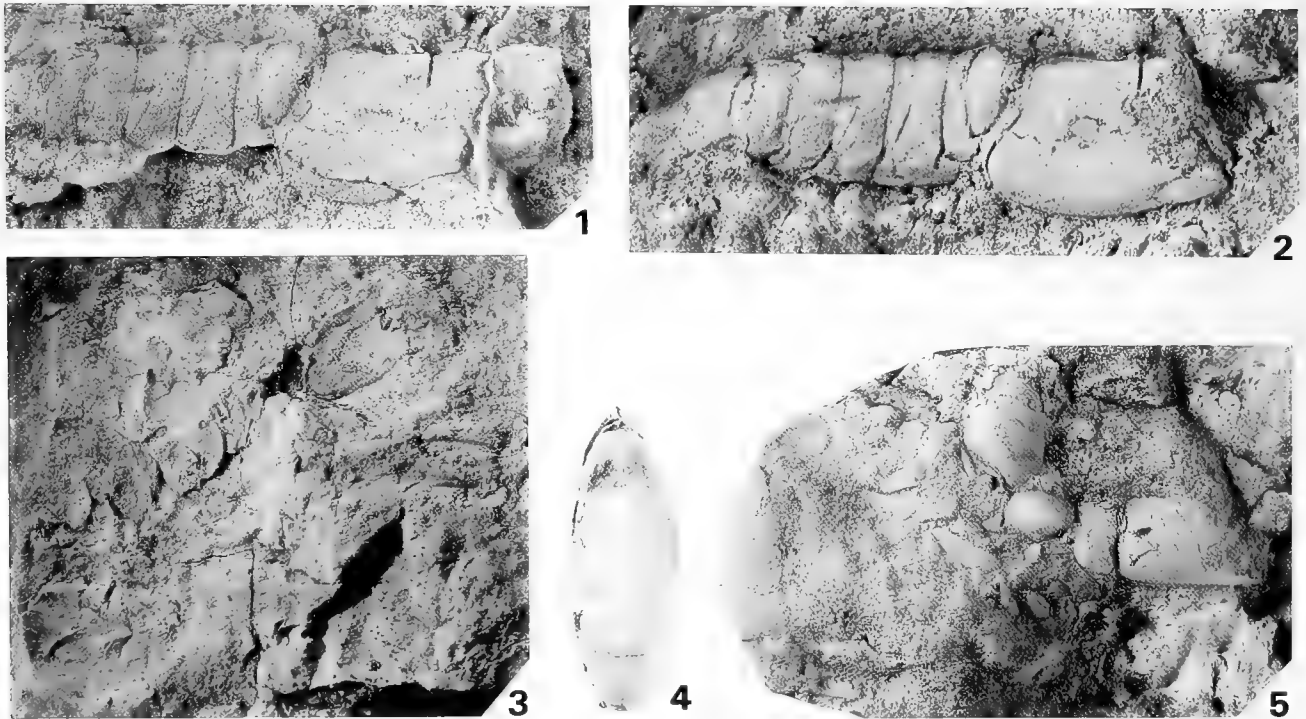


Figure 1. 1, 2. *Hoploparia* sp., MFM247111, carapace and abdomen. $\times 2.0$. 1: Latex cast of external mould of the specimen; 2: lateral view. 3–5. *Callianassa* (s. l.) *sakakuraorum* sp. nov. 3: MFM247016 (paratype), external mould of both chelipeds and abdomen, $\times 2.0$, lateral view. 4: MFM247015 (holotype), abdomen, $\times 2.0$, dorsal view. 5: MFM247015 (holotype), carapace, cheliped, pereopods and abdomen, $\times 2.0$, lateral view.

from the Hauterivian of Oregon. However, the present species has well developed supraorbital and antennal ridges on the carapace. *Hoploparia* sp. is similar to *Hoploparia longimana* (Sowerby, 1826) from the Barremian of Argentina and the Aptian-Cenomanian of England, and *Hoploparia mesembria* Etheridge, 1917 from the Albion of Australia, but differs in the presence of an obscurely defined hepatic groove and a well developed antennal ridge. *Hoploparia longimana* and *H. mesembria* possess a dentate supraorbital ridge and an antennal region with three large projections.

Hoploparia, earliest known from the Neocomian of Europe, U. S. A and Argentina (Aguirre-Urreta, 1989), has been recorded from Cretaceous-Palaeogene deposits in Europe, U. S. A, Japan, Argentina, Australia, New Zealand, and Antarctica (Aguirre-Urreta, 1989; Karasawa and Hayakawa, 2000).

Material examined.—MFM247111 collected by Y. Mizuno.

Infraorder Thalassinidea Latreille, 1831
Superfamily Callianassoidea Dana, 1852
Family Callianassidae Dana, 1852
Genus *Callianassa* Leach, 1814

***Callianassa* (s. l.) *sakakuraorum* sp. nov.**

Figure 1.3–1.5

Diagnosis.—Moderate-sized callianassid. Pereiopods 1 chelate, equal-sized, dissimilar. Palm of right cheliped, equal to fixed finger length, slightly longer than high; carpus short, about 1/4 propodus length, height 3/4 length; merus slightly longer than carpus, rhomboidal in lateral view, dorsal and ventral margins strongly convex without meral hook and spines. Propodus of left cheliped about equal to right propodus length, rather slender; palm slightly longer than fixed finger, height about 4/5 length.

Description.—Moderate sized callianassid. Only right branchial region of carapace preserved. Abdominal somite 1 poorly preserved. Somite 2 slightly longer than 3. Pleura of somites 2–5 well developed with rounded posteroventral corner. Pleuron of somite 6 reduced with convergent lateral margins. Telson about equal to length of somite 6 with longitudinal ridge on dorsal surface. Uropod unknown.

Pereiopods 1 chelate, equal-sized, dissimilar. Dactylus of right cheliped strongly curved ventrally with acutely pointed tip; dorsal and occlusal margins smooth. Fixed finger slightly longer than dactylus with acutely pointed tip; occlusal and ventral margins smooth. Palm rectangular in lateral view, equal to fixed finger length, slightly longer than high, with longitudinally convex lateral surface; dorsal and ventral margins smooth. Carpus short, about 1/4 propodus length, height 3/4 length, with nearly straight dorsal margin and strongly curved ventral margin. Merus slightly longer

than carpus, rhomboidal in lateral view, dorsal and ventral margins strongly convex without meral hook; lateral surface strongly vaulted. Ischium poorly preserved, slender without marginal teeth or spines. Propodus of left cheliped about equal to major propodus length, rather slender in outline, occupying about 3/4 major propodus height. Dactylus gently curved ventrally with acutely pointed tip; dorsal and occlusal margins smooth. Fixed finger slightly shorter than dactylus with acutely pointed tip; occlusal and ventral margin smooth. Palm rectangular in lateral view, slightly longer than fixed finger, height about 4/5 length, with smooth dorsal and ventral margins.

Pereiopod 2 not preserved. Carpus and merus of pereiopod 3 preserved; carpus flattened, slender, tapering proximally; merus flattened, about twice length of carpus with straight dorsal and gently convex ventral margins. Propodus, carpus, merus and ischium of pereiopod 4 preserved; propodus small, broken; carpus slender; merus about twice length of carpus; ischium about half carpus length. Pereiopod 5 unknown.

Discussion.—Manning and Felder (1991) recognized two families, seven subfamilies and 21 genera for taxa previously assigned to the extant Callianassidae, whilst Sakai (1999) reexamined all known extant members in the family and recognized four subfamilies and 10 genera. The generic placement of the present species awaits the discovery of better material bearing the maxilliped 3 and the telson, and it is considered best to place the specimen in *Callianassa* (s. l.) for the time being.

The genus *Callianassa* from the Cretaceous of Japan is represented by two species, "*Callianassa*" *ezoensis* Nagao, 1932 from the Maastrichtian Hakobuchi Sandstone and *Callianassa* (s. l.) *masanorii* Karasawa, 1998 from the Maastrichtian Izumi Group. *Callianassa* (s. l.) *sakakuraorum* differs from "*C.*" *ezoensis* in that pereiopods 1 have dissimilar chelipeds, smooth ventral margins of propodi, and a rhomboidal merus. Equal-sized pereiopods 1 with short fingers and carpi readily distinguish *C.* (s. l.) *sakakuraorum* from *C.* (s. l.) *masanorii*. The new species most resembles "*Callianassa*" *valida* Rathbun, 1935 from the Lower Cretaceous of Texas, but differs in having a shorter propodus of pereiopod 1 with a smooth dorsal margin and a rhomboidal merus of pereiopod 1. In *C.* (s. l.) *sakakuraorum* the dactylus of pereiopod 1 has a smooth dorsal margin whilst in "*C.*" *valida* it has a serrated dorsal margin.

The earliest known members of *Callianassa* (s. l.) have been recorded from the Neocomian of Europe (Glaessner, 1929) and the Valanginian of Argentina (Aguirre-Urreta, 1989). The Jurassic members of the genus were removed to the axiid genus *Etallonia* Oppel, 1861, by Förster (1977). The known distribution of *Callianassa* (s. l.) is from Upper Cretaceous–Recent worldwide (Glaessner, 1969).

Etymology.—The name is dedicated to Fujio and Norihiko Sakakura.

Material examined.—MFM247015 (holotype) collected by M. Chiba; MFM247016 (paratype) collected by N. Sakakura.

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Palaeogene decapod Crustacea from the Kishima and Okinoshima Groups, Kyushu, Japan

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Abstract. Twelve species in 11 genera of decapod crustaceans are recorded from Palaeogene rocks of Nagasaki and Saga Prefectures, Kyushu, Japan. *Carinocarcinoides* gen. nov. (Goneplacidae) is proposed to accommodate *Carinocarcinoides carinatus* sp. nov. and *Varuna angustifrons* Karasawa from the lower Oligocene Kishima Group. A new monotypic genus, *Cicarnus* (Portunidae), is erected with *Cicarnus fumiae* sp. nov. from the middle Eocene Okinoshima Group. *Neocallichirus sakiae* sp. nov. (Callianassidae) is described from the lower Oligocene Kishima Group. *Axius* (s. l.) sp. and *Euphyllax* ? sp. from the Kishima Group represent the first records for both genera from the Oligocene of Japan. The occurrence of *Minohellenus macrocheilus* Kato and Karasawa extends the known geologic range of this species back to the lower Oligocene. A new description is given for *Collinsius simplex* Karasawa.

Key words: Crustacea, Decapoda, Japan, Kyushu, Palaeogene

Introduction

Previous contributions describing and illustrating decapod species from Palaeogene rocks of Kyushu are rather limited. Yokoyama (1911) was the first to describe two new species, *Xanthilites pentagonalis* and *Homolopsis japonicus*, from the Palaeogene of the Miike Coalfield. Nagao (1941) recorded and illustrated an unnamed *Callianassa* sp. indet. from the Palaeogene of the Asakura Coalfield. Five species in five genera were described from the lower Oligocene Kishima Group in Saga and Nagasaki Prefectures by Imaizumi (1958) and Karasawa (1993, 1997). Inoue (1972) introduced an abundant occurrence of unnamed crabs from the lower Oligocene Kishima Group distributed in the Karatsu Coalfield. Karasawa (1992) described five species from the middle Eocene Manda Group, moved *Xanthilites pentagonalis* to *Branchioplax* Rathbun, 1916 and erected a new monotypic genus *Prohomola* for *Homolopsis japonicus*. Kato and Karasawa (1994) described a new portunid, *Minohellenus macrocheilus* from the upper Oligocene Ashiya Group and additional material of the species was recorded (Kato and Karasawa, 1996).

The purpose of this paper is to describe 12 species in 11 genera, including two new genera and three new species, of decapods from the middle Eocene-lower Oligocene rocks in Saga and Nagasaki Prefectures, Kyushu. New descriptions are given for *Carinocarcinoides angustifrons* (Karasawa, 1993) comb. nov. and *Collinsius simplex* Karasawa, 1993.

The specimens described in the paper are housed in the Mizunami Fossil Museum (MFM).

Localities

Kosasa area (Figure 1A)

Imaizumila sexdentata Karasawa, 1993 occurred in sandstone of the Nagashima Sandstone Member, Haiki Formation, Kishima Group exposed at Takasakiyama (Loc. KSM-1), Usunoura, Kosasa-cho, Kitamatsura-gun, Nagasaki Prefecture. The Haiki Formation was correlated with the Hatatsu Sandstone Member and Yukiaino Sandstone Member of the Kishima Group distributed in the Karatsu-Taku areas (Matsui *et al.*, 1989). According to Okada (1992), the Hatatsu Sandstone Member and Yukiaino Sandstone Member are assigned to Zone CP17 (early Oligocene) of Okada and Bukry's (1980) scale of nannofossils.

Karatsu-Taku areas (Figure 1B)

Eight species in seven genera of decapods (Figure 2) were collected from the Kishima Formation and Yukiaino Sandstone Member of the Kishima Group from 15 localities distributed in the eastern part of Saga Prefecture. Okada (1992) assigned the Kishima Formation to Zone CP16a of Okada and Bukry's nannozones and the Yukiaino Sandstone to Zone CP17. Details of localities are shown in Table 1.

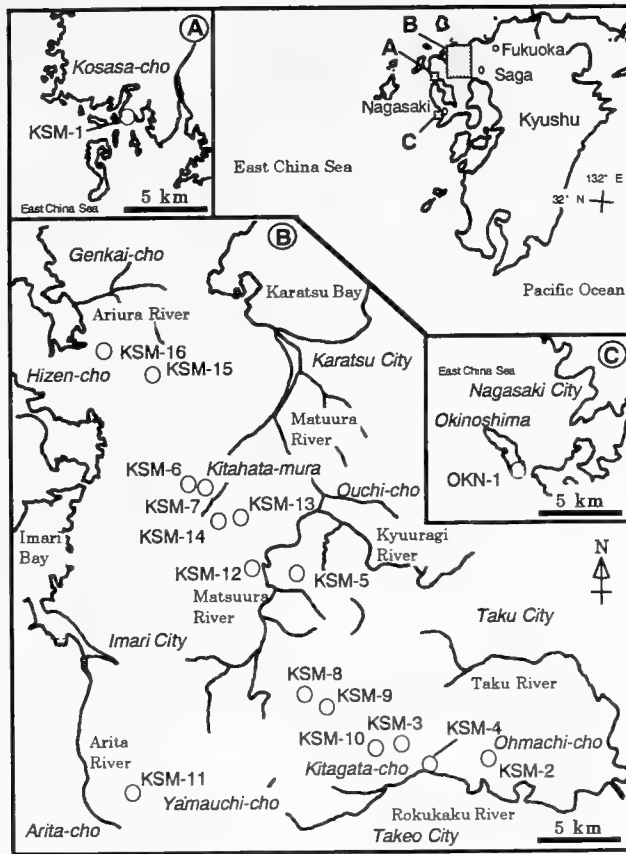


Figure 1. Map showing decapod localities of the studied areas.

Okinoshima area (Figure 1C)

Three species in three genera of decapods (Figure 2) were collected from sandstone of the Okinoshima Formation of the Okinoshima Group exposed at Aze, Iojima-cho, Nagasaki City. The Okinoshima Formation is correlated with the lower part of the Sakasesgawa Group in the Amakusa Coalfield and the Nougata Group in the Chikuho Coalfield (Ozaki and Hamasaki, 1991). According to Ozaki and Hamasaki, the formation seems to be assigned to Zones CP13–14 (middle Eocene) by Okada and Bukry's (1980) nannozone.

Summary of the Palaeogene decapod fauna of Kyushu

The decapod fauna from the Okinoshima Group comprises three species, *Callianassa* (s. l.) sp., *Raninoides nodai* Karasawa, 1992 and *Cicarnus fumiae* gen. et sp. nov. (Figure 2). Previously known decapods from the middle Eocene rocks are recorded from the Dosi and Kawamagari Formations (Nagao, 1941) and the Manda Group (Yokoyama, 1911; Karasawa, 1992). *Callianassa* (s. l.) sp. is known from the Dosi and Kawamagari Formations and *R. nodai* from the Manda Group. *Cicarnus* is only known from the Okinoshima Group. The middle Eocene decapod fauna has close affinities with those of the western-central Tethys region, based on the occurrences of *Prohomola*, *Portunites* and *Branchiopanax* from the Manda Group (Karasawa, 1992, 1999).

The early Oligocene decapod fauna from the Kishima Group is represented by nine species in eight genera (Figure 2). The fauna from the Kishima Formation is characterized by the abundant occurrence of *Collinsius simplex* Karasawa, 1993, whilst from the Yukiaino Sandstone Member it is char-

| Species | Age | Middle Eocene | Early Oligocene | | | | | | | | | | | | | | | | |
|---|------------------------------------|---------------|-------------------|---|---|---|---|---|---|---|----|----|-----------------------|----|----|----|----------|---|--|
| | Nanno Zone by Okada & Bukry (1980) | CP13-14 | CP16a | | | | | | | | | | CP17 | | | | | | |
| | Formation | Okinoshima G. | Kishima Group | | | | | | | | | | | | | | | | |
| | | Okinoshima F. | Kishima Formation | | | | | | | | | | Yukiaino Sandstone M. | | | | Haiki F. | | |
| | Locality | OKN-1 | KSM- | | | | | | | | | | | | | | | | |
| | | | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 1 | |
| <i>Axius</i> (s.l.) sp. | | | | | | X | | | | | | | | | | | | | |
| <i>Ctenocheles sujakui</i> Imaizumi, 1958 | | X | X | X | | | X | | | | | | | | | | | | |
| <i>Callianassa</i> (s.l.) sp. | X | | | | | | | | | | | | | | | | | | |
| <i>Neocallichirus sakiae</i> sp. nov. | | | | | | | | | | | | X | X | X | X | X | | | |
| <i>Raninoides nodai</i> Karasawa, 1992 | X | | | | | | | | | | | | | | | | | | |
| <i>Imaizumila sexdentata</i> Karasawa, 1993 | | | | | | | | | | | | | | | | | X | | |
| <i>Cicarnus fumiae</i> gen. et sp. nov. | X | | | | | | | | | | | | | | | | | | |
| <i>Minohellenus macrocheilus</i> Kato and Karasawa, 1994 | | | | | | X | | | | | | | | | | X | | | |
| <i>Euphyllax</i> ? sp. | | | X | | | | | | | | | | | | | | | | |
| <i>Carinocarcinoides angustifrons</i> (Karasawa, 1993) comb. nov. | | X | | | | | | | | | | | | | | | | | |
| <i>Carinocarcinoides carinatus</i> gen. et sp. nov. | | | | | | | | | X | | | | | | | | | | |
| <i>Collinsius simplex</i> Karasawa, 1993 | | X | X | X | X | X | X | X | X | X | X | | | | | | | | |

Figure 2. List of fossil decapods from the studied areas. Locality numbers are shown in Figure 1.

Table 1. List of decapod-bearing localities of the Karatsu-Taku areas.

| Loc. no. | Locality | Formation |
|----------|---|---|
| KSM-2 | Hatada, Ohmachi, Ohmachi-cho, Saga Prefecture | Sandy mudstone of the Kishima Formation, Kishima Group |
| KSM-3 | Magami, Osaki, Kitagata-cho, Saga Prefecture | Sandy mudstone of the Kishima Formation, Kishima Group |
| KSM-4 | SE of Magami, Osaki, Kitagata-cho, Saga Prefecture | Sandy mudstone of the Kishima Formation, Kishima Group |
| KSM-5 | Tatsugawa, Okawa-cho, Imari City, Saga Prefecture | Sandy mudstone of the Kishima Formation, Kishima Group |
| KSM-6 | Shimohirano, Kitahata-mura, Saga Prefecture | Sandy mudstone of the Kishima Formation, Kishima Group |
| KSM-7 | Shimohiranotoge, Kitahata-mura, Saga Prefecture | Sandy mudstone of the Kishima Formation, Kishima Group |
| KSM-8 | Sarajuku, Takeo City, Saga Prefecture | Sandy mudstone of the Kishima Formation, Kishima Group |
| KSM-9 | Wakagi, Takeo City, Saga Prefecture | Sandy mudstone of the Kishima Formation, Kishima Group |
| KSM-10 | Takatori, Kitagata-cho, Saga Prefecture | Sandy mudstone of the Kishima Formation, Kishima Group |
| KSM-11 | Oubounotoge, Arita-cho, Saga Prefecture | Sandy mudstone of the Kishima Formation, Kishima Group |
| KSM-12 | Komanaki, Okawa-cho, Imari City, Saga Prefecture | Sandstone of the Yukiaino Sandstone Member, Kishima Group |
| KSM-13 | Shige, Kitahata-mura, Saga Prefecture | Sandstone of the Yukiaino Sandstone Member, Kishima Group |
| KSM-14 | Tuzumi, Minamihata-cho, Imari City, Saga Prefecture | Sandstone of the Yukiaino Sandstone Member, Kishima Group |
| KSM-15 | Kirigo, Hizen-cho, Saga Prefecture | Sandstone of the Yukiaino Sandstone Member, Kishima Group |
| KSM-16 | Sosorogawachi, Genkai-cho, Saga Prefecture | Sandstone of the Yukiaino Sandstone Member, Kishima Group |

acterized by the frequent occurrence of *Neocallichirus sakiae* sp. nov. Among the known genera from the Kishima Group, *Carinocarcinoides* and *Collinsius* are Japanese early Oligocene endemic genera; *Imaizumila* is only known from the Oligocene of Japan and the Eocene-Miocene of Chile (Schweitzer and Feldmann, 2000); *Minohellenus* occurs outside of Japan in Oligocene-Miocene rocks of Washington and Oregon (Schweitzer and Feldmann, 2000). *Axius* (s. l.), *Ctenocheles*, *Callianassa* (s. l.) and *Neocallichirus* are cosmopolitan. *Euphyllax* occurs in the Caribbean and East Pacific Ocean at the present day, but the fossil record seems to extend to the lower Oligocene of Japan. Karasawa (1999) suggested that the Tethyan genera *Prohomola*, *Portunites* and *Branchioplax* disappeared by the Oligocene and that the decapod fauna of southwest Japan appears to become endemic in the early Oligocene.

Systematic paleontology

Infraorder Thalassinidea Latreille, 1831
 Superfamily Axiodea Huxley, 1879
 Family Axiidae Huxley, 1879
 Genus *Axius* Leach, 1814

Type species.—*Axius stirhynchus* Leach, 1814 by monotypy.

Geologic range.—Oligocene to Recent.

Axius (s. l.) sp.

Figure 3.1a–c

Description.—Anterior half of carapace preserved but lacks rostrum. Anterolateral margin unarmed. Gastric region convex; median carina smooth, well marked, extending from anterior margin to posterior fourth of gastric region; lat-

eral carinae weak, extending from anterior margin to anterior third of gastric region. Cervical groove well developed, reaching anteroventrally to hepatic region. Postcervical region of carapace glabrous. Pereiopods 1–3 preserved. Meri of both pereiopods 1 flattened laterally, lateral surface smooth, dorsal and ventral margins pitted, without spines. Palm and carpus of pereiopod 2 compressed laterally; lateral surface, dorsal and ventral margins smooth. Carpus and merus of pereiopod 3 cylindrical in cross section, without marginal spines.

Discussion.—Poore (1994) recognized four families and 32 genera for taxa previously assigned to the extant Axiidae. The definition of the extant axiids includes detailed characters of eyes, antennae, pleopods, and uropods, which are not available for study in fossil specimens. The present species is assigned to *Axius* (s. l.) by having a carapace with a well defined cervical groove and without *linea thalassinicae*. The single incomplete specimen renders generic placement obscure and it is considered best to place the specimen in *Axius* (s. l.).

Previously known fossil members of *Axius* (s. l.) are recorded from the Oligocene of Panama and the Pliocene of France (Glaessner, 1969).

Material examined.—MFM218633 from KSM-6.

Superfamily Callianassoidea Dana, 1852
 Family Ctenochelidae Manning and Felder, 1991
 Subfamily Ctenochelinae Manning and Felder, 1991
 Genus *Ctenocheles* Kishinoue, 1926

Type species.—*Ctenocheles balssi* Kishinoue, 1926 by monotypy.

Geologic range.—Late Cretaceous to Recent.

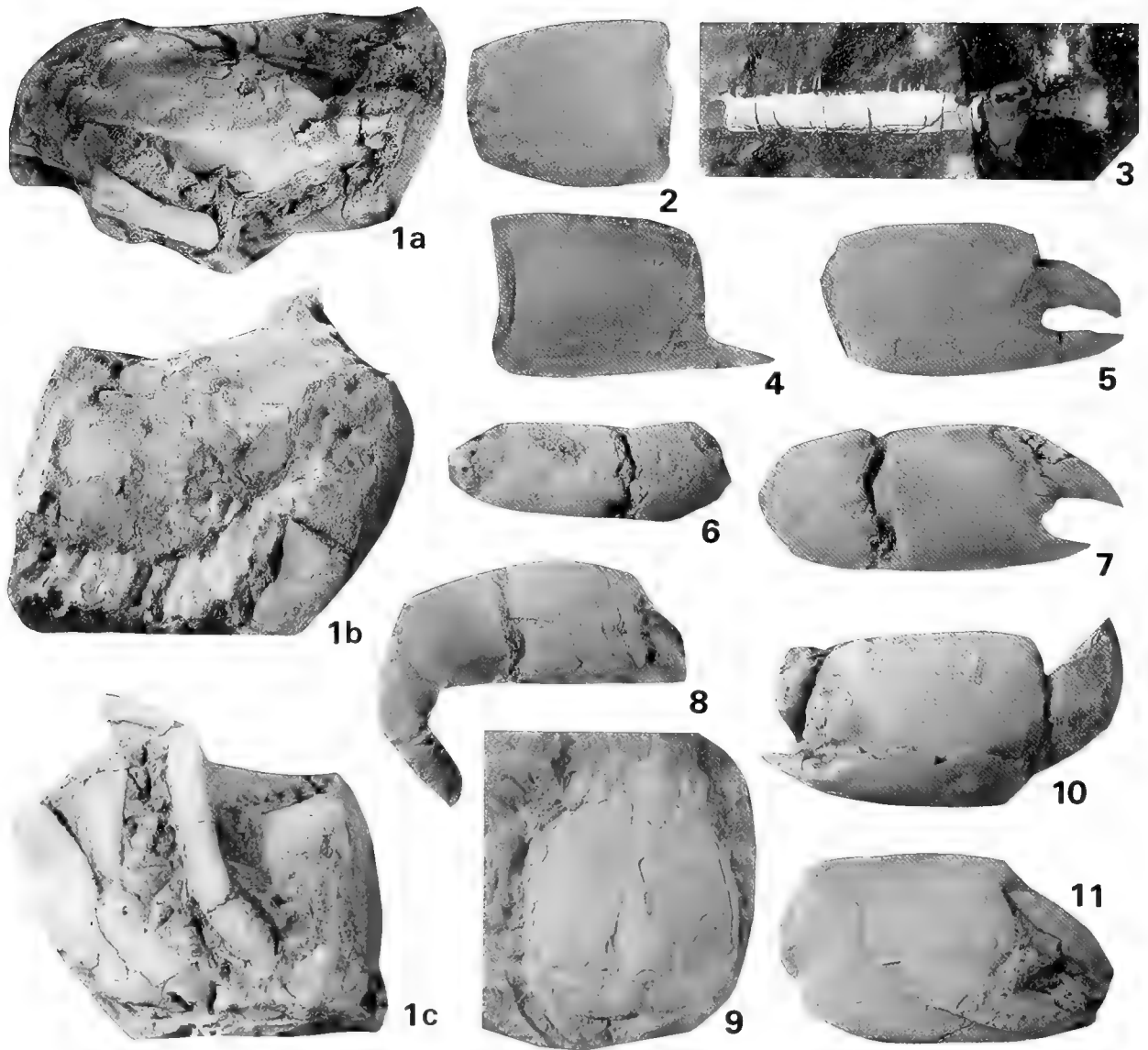


Figure 3. 1a–c. *Axius* (s. l.) sp., MFM218633, $\times 1.8$; 1a: carapace, dorsal view; 1b: carapace and pereopod 1, lateral view; 1c: carapace and pereopods 1–3, lateral view. 2, 4. *Callianassa* (s. l.) sp., $\times 1.2$; 2, carpus of major cheliped, lateral view; 4: propodus of major cheliped, mesial view. 3. *Ctenocheles sujakui* Imaizumi, 1958, MFM218631, fixed finger of major cheliped, $\times 1.8$, lateral view. 5–8, 10, 11. *Neocallichirus sakiae* sp. nov.; 5: MFM218516 (paratype), major cheliped, $\times 1.5$, lateral view; 6: MFM218515 (holotype), minor cheliped, $\times 2.5$, lateral view; 7: MFM218519 (paratype), major cheliped, $\times 1.5$, lateral view; 8: MFM218515 (holotype), major cheliped, $\times 1.5$, lateral view; 10: MFM218518 (paratype), major cheliped, $\times 1.5$, lateral view; 11: MFM218517 (paratype), major cheliped, $\times 1.5$, lateral view. 9: *Raninoides nodai* Karasawa, 1992, MFM218636, carapace, $\times 1.5$, dorsal view.

***Ctenocheles sujakui* Imaizumi, 1958**

Figure 3.3

Ctenocheles sujakui Imaizumi, 1958, p. 301, pl. 44, figs. 2–5;
Karasawa, 1997, p. 31, pl. 3, figs. 5, 7.

Remarks.—Imaizumi (1958) originally described the species from the lower Oligocene Kishima Formation of Nagao, Taku City, Saga Prefecture.

Material examined.—MFM218631 and 218632 from KSM-3; referred specimens from KSM-2, 4, 7.

Family Callianassidae Dana, 1852
Subfamily Callianassinae Dana, 1852

Remarks.—Manning and Felder (1991) recognized two families, seven subfamilies and 21 genera for taxa previously assigned to the extant Callianassidae. According to Manning and Felder's (1991) classification, Poore (1994) gave keys to 20 genera in the extant Callianassidae. Since then, four genera, *Grynaminna* Poore, 2000, *Necallianassa* Heard and Manning, 1998, *Nihonotrypaea* Manning and Tamaki, 1998, and *Pseudobiffarius* Heard and Manning, 2000, have been described. Fossil taxa have traditionally been assigned to *Callianassa* (s. l.); however, recent studies have employed the classification of Manning and Felder (Karasawa, 1992, 1993, 1997; Karasawa and Goda, 1996; Kato, 1996; Schweitzer Hopkins and Feldmann, 1997; Stilwell *et al.*, 1997; Vega *et al.*, 1995). Sakai (1999) reexamined all known extant members in the family Callianassidae and recognized four subfamilies and 10 genera in the family. The classification of Callianassidae by Sakai is quite different from Manning and Felder's (1991) system. After that, Sakai and Türkay (1999) erected a new subfamily Bathycalliacinae with a new genus *Bathycalliax*. Therefore, the fossil species referred to the Callianassidae are in need of reexamination.

Genus *Callianassa* Leach, 1814

Type species.—*Cancer (Astacus) subterraneus* Montagu, 1808 by monotypy.

Geologic range.—Cretaceous to Recent.

Callianassa (s. l.) sp.

Figure 3.2, 3.4

Callianassa sp. indet.; Nagao, 1941, p. 85, pl. 26, figs. 8, 9.

Description.—Propodus and carpus of major cheliped preserved. Fixed finger short, about 0.3 propodus length, with acutely pointed tip. Palm subrectangular in lateral view, longer than high, with distally convergent dorsal and ventral margins. Carpus subrectangular in lateral view, equal to palm length; dorsal and ventral margins divergent distally.

Discussion.—The generic placement of the present species awaits the discovery of better material and it is considered best to place the species in *Callianassa* (s. l.). The known Japanese Palaeogene species formerly placed in the genus *Callianassa* comprise five species, *Callianassa elongatodigitata* Nagao, 1941, *Callianassa isikariensis* Nagao and Ôtsume, 1938, *Callianassa kushiroensis* Nagao, 1941 and *Callianassa muratai* Nagao, 1932 of Hokkaido, and *Callianassa* sp. indet. (Nagao, 1941) of Kyushu. Among these, *C. muratai* and *C. elongatodigitata* were moved to the genus *Callianopsis* De Saint Laurent, 1973 in the family Ctenochelidae by Kato and Karasawa (1994). The present species differs from *C. isikariensis* and *C. kushiroensis* in that the major cheliped has a short fixed finger and a palm with distally convergent dorsal and ventral margins. The species is identical with *Callianassa* sp. indet. described from the middle Eocene Dosi and

Kawamagari Formations of Fukuoka Prefecture by Nagao (1941).

Material examined.—MFM218634 and 218635 from OKN-1.

Subfamily Callichirinae Manning and Felder, 1991
Genus *Neocallichirus* Sakai, 1988

Type species.—*Neocallichirus horneri* Sakai, 1988 by original designation.

Geologic range.—Oligocene to Recent.

Neocallichirus sakiae sp. nov.

Figure 3.5–3.8, 3.10, 3.11

Etymology.—The specific name is in honor of Miss Saki Fudouji.

Diagnosis.—Chelipeds large, unequal, dissimilar. Dorsal margin of dactylus of major cheliped smooth; occlusal margin with broad tooth on midlength. Fixed finger shorter than dactylus; occlusal margin with broad tooth on proximal half. Palm rectangular, about 1.3 times longer than high, 1.3 propodus length, with serrated distal margin. Carpus subrectangular, about 0.6 palm length, slightly higher than long. Merus equal to palm length, about 0.6 times higher than long; ventral margin strongly convex without ventral hook. Ischium with dentate ventral margin.

Description.—Chelipeds large in size, unequal, dissimilar. Dactylus of major cheliped curved ventrally with acutely pointed tip; dorsal margin smooth with 4 setal pits; occlusal margin bearing broad tooth at midlength; lateral surface inflated with 4 setal pits parallel to occlusal margin. Fixed finger about 0.75 dactylus length with acutely pointed tip; occlusal margin bearing broad tooth on proximal half; ventral margin smooth; lateral surface slightly convex with row of setal pits parallel occlusal and ventral margins. Palm rectangular in lateral view, about 1.3 times longer than high, 1.3 propodus length; dorsal margin slightly convex; ventral margin nearly straight; distal margin gently convex, serrate; lateral surface longitudinally inflated with row of setal pits parallel to ventral margin. Carpus subrectangular in lateral view, about 0.6 palm length, slightly higher than long, tapering proximally, with convex lateral surface. Merus equal to palm length, about 0.6 times higher than long; dorsal margin gently convex; ventral margin strongly convex without ventral hook; lateral surface with longitudinal ridge. Ischium poorly preserved, about as long as merus, ventral margin dentate.

Fingers of minor cheliped poorly preserved. Palm rectangular in lateral view, occupying about half palm length of major cheliped, slightly longer than high, with convex lateral surface; dorsal margin smooth, ventral margin pitted. Carpus rectangular, about 0.75 palm length, with convex lateral surface, its length equal to height.

Discussion.—The Japanese fossil *Neocallichirus* is represented by three species, *Neocallichirus bona* (Imaizumi, 1959) from the Miocene Moniwa Formation and Mizunami Group (Karasawa, 1993, 1997), *Neocallichirus grandis* Karasawa and Goda, 1996, from the middle Pleistocene Atsumi Group (Karasawa and Goda, 1996) and the middle-

upper Pleistocene Shimosa Group (Kato and Karasawa, 1998), and *Neocallichirus okamotoi* (Karasawa, 1993) from the upper Oligocene Hioki Group (Karasawa, 1993, 1997). Among these, the new species most resembles *N. okamotoi* but differs in that the major cheliped has broad teeth on the occlusal margin of both fingers, a longer palm with a serrated, convex distal margin and a shorter carpus. The merus on the major cheliped without marginal denticles and a short merus readily distinguish *N. sakiae* from *N. bona* and *N. grandis*.

Material examined.—MFM218515 (holotype) and 218516 (paratype) from KSM-12; MFM218517 (paratype) and 218518 (paratype) from KSM-16; MFM218519 (paratype) from KSM-14; referred specimens from KSM-13, 14, 15.

Infraorder Brachyura Latreille, 1802
Section Podotremata Guinot, 1977
Superfamily Raninoidea De Haan, 1841
Family Raninidae De Haan, 1841
Subfamily Raninoidinae Lörentz in Lörentz
and Beurlen, 1929
Genus ***Raninoides*** H. Milne Edwards, 1837

Type species.—*Ranina loevis* Latreille, 1825 by monotypy.

Geologic range.—Palaeocene to Eocene.

Raninoides nodai Karasawa, 1992

Figure 3.9

Raninoides nodai Karasawa, 1992, p. 1252, figs. 4.2–4.8;
Karasawa, 1997, p. 39, pl. 7, figs. 7, 9, 11.
Laeviranina nodai (Karasawa); Tucker, 1998, p. 351.

Remarks.—Tucker (1998) provisionally placed *Raninoides nodai* in *Laeviranina* Lörentz in Lörentz and Beurlen, 1929. However, this species should be assigned to *Raninoides* based upon the absence of the postfrontal ridge on the carapace.

Material examined.—MFM218636 from OKN-1.

Section Heterotremata Guinot, 1977
Superfamily Portunoidea Rafinesque, 1815
Family Portunidae Rafinesque, 1815
Subfamily Carcininae MacLeay, 1838
Genus ***Cicarnus*** gen. nov.

Type species.—*Cicarnus fumiae* sp. nov. by monotypy.

Etymology.—*Cicarnus* is an anagram of *Carcinus* Leach, 1814; masculine gender.

Diagnosis.—Carapace transversely hexagonal in outline, length about 0.8 its width. Orbitofrontal margin wide. Front with 3 rounded lobes, separated from small, bluntly triangular supraorbital angle by shallow V-shaped notch. Upper orbital margin with 2 open fissures. Anterolateral margin convex, bearing 4 well developed teeth. Dorsal surface smooth, moderately convex. Regions well defined. Epigastric region transversely raised anteriorly. Proto-gastric region inflated with transverse ridge on each side. Mesogastric region bearing anterior transverse ridge.

Cervical groove well defined. Epibranchial region more inflated. Branchiocardiac grooves poorly defined.

Discussion.—The subfamily Carcininae is defined by the following characters: The carapace is not broad with four or five anterolateral teeth; chelae are short; pereopods 2–5 are similar and rather stout, and the pereopod 5 has a lanceolate dactylus [modified from Glaessner (1969)]. Although carapace characters of Carcininae overlap those of the subfamily Polybiinae Ortmann, 1893, Polybiinae are distinguished from Carcininae by having a paddle-like pereopod 5 (Glaessner, 1969; Schweitzer and Feldmann, 2000).

The Recent Carcininae comprises six genera, *Benthochascon* Alcock and Anderson, 1899, *Brusinia* Štefčić, 1991, *Carcinus* Leach, 1814, *Nectocarcinus* A. Milne Edwards, 1860, *Portumnus* Leach, 1814 and *Xaiva* MacLeay, 1838 (Moosa, 1996). Three extinct genera, *Portunites* Bell, 1858, *Pleolobites* Remy, 1960 and *Mioxaiva* Müller, 1979, were previously assigned to the subfamily (Glaessner, 1969; Müller, 1979). Schweitzer and Feldmann (2000) and Schweitzer *et al.* (2000) removed *Portunites* to Polybiinae based upon the presence of a paddle-like pereopod 5. The position of *Pleolobites* and *Mioxaiva* within Carcininae is doubtful (Glaessner, 1969; Müller, 1984).

The present new genus and species are represented by a single carapace specimen, and chelipeds and pereopods are not preserved. However, *Cicarnus* possesses carapace characters most like those of *Benthochascon*, *Carcinus* and *Nectocarcinus*, and may be assigned to Carcininae. *Cicarnus* is most similar to *Nectocarcinus*, but differs in having well developed anterolateral teeth, the frontal margin composed of three rounded lobes, and a smooth dorsal carapace. The mesogastric region in *Cicarnus* has a transverse ridge interrupted by a shallow median groove. With respect to the front which is composed of three rounded lobes, the new genus resembles *Benthochascon* and *Carcinus*. *Cicarnus* differs from *Carcinus* in having four anterolateral teeth and well defined dorsal regions. Although *Cicarnus* together with *Benthochascon* bears four anterolateral teeth, in *Cicarnus* the dorsal regions are well defined and a wide anterolateral margin bears well separated teeth.

Cicarnus fumiae sp. nov.

Figure 4.2a–c

Etymology.—The specific name is in honor of Mrs. Fumie Karasawa.

Diagnosis.—As for the genus.

Description.—Carapace hexagonal in outline, length about 0.8 its width. Orbitofrontal margin wide, occupying 0.6 carapace width. Front composed of 3 rounded lobes, occupying about 0.3 carapace width, separated from small, bluntly triangular supraorbital angle by shallow V-shaped notch; median frontal lobe small and laterals broad. Upper orbital margin concave, bearing shallow fissure at about midwidth of orbit and shallower fissure anterior to outer orbital tooth. Anterolateral margin convex, occupying about 0.45 carapace width, bearing 4 well separated teeth including outer orbital tooth; outer orbital tooth acutely triangular,

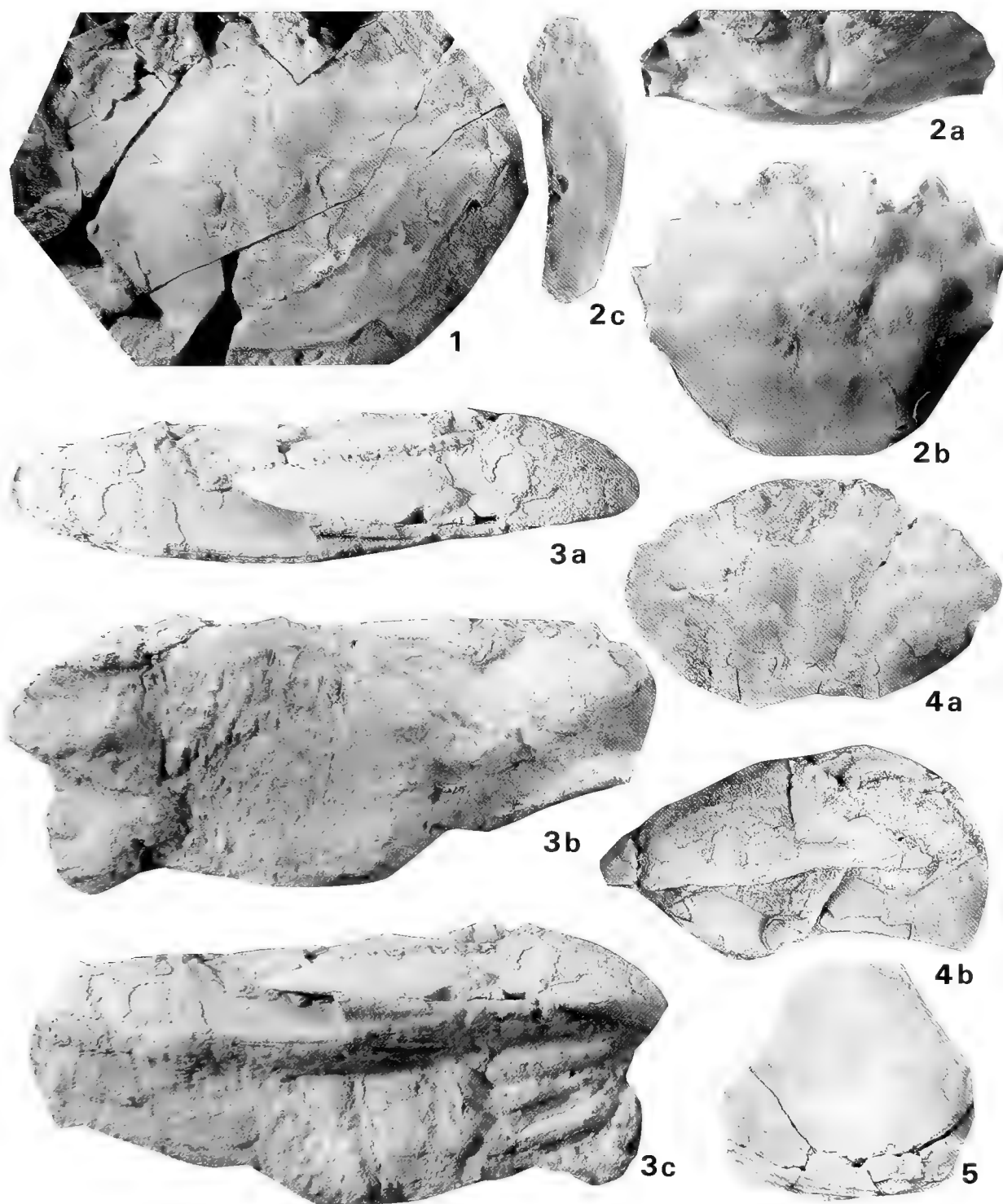


Figure 4. 1. *Imaizumila sexdentata* Karasawa, 1993, MFM218507 (holotype), carapace, $\times 1.2$, dorsal view. 2a–c. *Cicarnus fumiae* gen. et sp. nov., MFM218512 (holotype), $\times 1.5$, 2a: frontal view; 2b: dorsal view; 2c: lateral view. 3a–c. *Euphyllax* ? sp., MFM218639, $\times 1.0$; 3a: both chelipeds, lateral view; 3b: carapace, cheliped and pereopods, dorsal view; 3c: thoracic sternum, chelipeds and pereopods, ventral view. 4a, b, 5. *Minohellenus macrocheilus* Kato and Karasawa, 1994, $\times 1.2$; 4a: MFM218637, carapace, dorsal view; 4b: MFM218637, right cheliped, lateral view; 5: MFM218638, carapace, dorsal view.

directed anteriorly; second broadly triangular, slightly directed anterolaterally and dorsally; third acutely triangular, directed anterolaterally and dorsally; last lacking tip, but directed laterally and dorsally. Posterolateral margin sinuous, slightly longer than anterolateral margin. Posterior margin nearly straight, slightly longer than posterolateral margin.

Dorsal surface smooth, moderately convex, with well defined regions. Epigastric region transversely raised anteriorly. Protogastric region inflated, well separated from narrow anterior mesogastric process, with transverse ridge on each side. Mesogastric region convex, pentagonal in outline, bearing anterior transverse ridge divided into two by shallow median depression. Urogastric region narrow, depressed. Cervical groove well defined. Cardiac region slightly convex, hexagonal in outline, bearing two nodes transversely arranged. Intestinal region depressed. Hepatic region slightly convex. Epibranchial region more inflated, shallowly separated from mesobranchial region. Meso- and metabranchial regions also inflated. Branchio-cardiac grooves poorly defined.

Discussion.—As for the genus.

Material examined.—MFM218512 (holotype) from OKN-1.

Subfamily Polybiinae Ortmann, 1893
Genus *Imaizumila* Karasawa, 1993

Type species.—*Imaizumila sexdentata* Karasawa, 1993 by monotypy.

Geologic range.—Eocene to Middle Miocene.

Imaizumila sexdentata Karasawa, 1993

Figure 4.1

Imaizumila sexdentata Karasawa, 1993, p. 52, pl. 11, figs. 1–3; Karasawa, 1997, p. 48, pl. 11, figs. 8, 12.

Remarks.—Previously specimens were recorded only from the lower Oligocene Haiki Formation of the Kishima Group (Karasawa, 1993). Schweitzer and Feldmann (2000) described an additional species, *Imaizumila araucana* (Philippi, 1887) from the Eocene-Miocene of Chile.

Material examined.—MFM218507 (holotype) and 218508 (paratype) from KSM-1.

Genus *Minohellenus* Karasawa, 1990

Type species.—*Charybdis (Minohellenus) quinquedentata* Karasawa, 1990 by monotypy.

Geologic range.—Early Oligocene to Middle Miocene.

Minohellenus macrocheilus Kato and Karasawa, 1994

Figure 4.4a, b, 4.5

Minohellenus macrocheilus Kato and Karasawa, 1994, p. 55, fig. 2; pl. 4, figs. 1–4; Kato and Karasawa, 1996, p. 31, pl. 10, figs. a–c; Karasawa, 1997, p. 49, pl. 14, figs. 2–7.

Remarks.—Previously known specimens were recorded from the upper Oligocene Ashiya Group (Kato and

Karasawa, 1994, 1996). The discovery of *M. macrocheilus* from the Kishima Group extends the geologic range for the species back to the early Oligocene.

Material examined.—MFM218637 from KSM-16; MFM 218638 from KSM-6.

Subfamily Podophthalminae Miers, 1886
Genus *Euphyllax* Stimpson, 1860

Type species.—*Euphyllax dovii* Stimpson, 1860 by monotypy.

Geologic range.—Oligocene to Recent.

Euphyllax ? sp.

Figure 4.3a–c

Description.—Right half of carapace poorly preserved; upper orbital margin wide, gently convex; anterolateral margin narrow with laterally directed stout spine; posterolateral margin sinuous. Thoracic sternum wide, sternites 4–7 preserved.

Chelipeds similar. Dactylus slender, elongate, with smooth dorsal margin and irregularly dentate opposing margin. Fixed finger elongate, about 0.3 times higher than long proximally, with acutely pointed tip; occlusal margin straight, irregularly dentate; ventral margin convex, smooth. Palm short, about 0.75 fixed finger length, about 0.6 times longer than high, converging proximally; dorsal surface tuberculated; ventral margin smooth.

Meri of pereopods 2 and 3 ovate in cross section.

Discussion.—There is, in the general outline of chelipeds, similarity between the species and *Euphyllax domingensis* (Rathbun, 1919) from the lower Miocene? of Haiti, but this species has a slender dactylus and a short palm without carinae on the lateral margin. However, a well preserved carapace of this species is needed to qualify the systematic position.

Material examined.—MFM218639 from KSM-3.

Superfamily Xanthoidea MacLeay, 1838

Family Goneplacidae MacLeay, 1838

Subfamily Carcinoplacinae H. Milne Edwards, 1852

Carinocarcinoides gen. nov.

Type species.—*Carinocarcinoides carinatus* sp. nov. by present designation.

Etymology.—The genus is named in allusion to its close resemblance to *Carinocarcinus* Lørenthey, 1898; masculine gender.

Diagnosis.—Carapace transversely hexagonal to roundly quadrate in outline, widest at anterolateral angle. Orbitofrontal margin wide. Front nearly straight with sharply squared corners. Upper orbital margin concave with triangular, forwardly directed outer orbital spine and without fissures. Inner suborbital tooth sharp, projecting anteriorly. Anterolateral margin strongly convex with 2 small, anterolaterally directed spines exclusive of outer orbital spine. Dorsal surface smooth, moderately vaulted transversely and weakly vaulted longitudinally. Regions distinct. Protogastric, cardiac and epigastric ridges present.

Anterior mesogastric process poorly defined. Cervical and branchiocardiac grooves well defined. Thoracic sternum narrow, longer than wide, tapering anteriorly and posteriorly. Chelipeds large; dactylus, palm and carpus finely granulate on dorsal and lateral surfaces.

Discussion.—*Carinocarcinoides* possesses characters most like those of the extant genera *Carcinoplax* H. Milne Edwards, 1852 and *Homoioplax* Rathbun, 1914. However, *Carinocarcinoides* has a dorsal carapace with well defined regions and several ridges. The thoracic sternum of the new genus is much narrower than that of *Carcinoplax*. Of the extinct genera within Carcinoplacinae, *Carinocarcinoides* is most similar to *Carinocarcinus* Lörentz, 1898, a monotypic genus from the middle Eocene of Hungary, but differs in having a straight front with sharp lateral corners, three anterolateral teeth including the outer orbital spine, and a protogastric ridge.

The new genus is represented by two species, *Carinocarcinoides angustifrons* (Karasawa, 1993) comb. nov. and *Carinocarcinoides carinatus* sp. nov., from the lower Oligocene Kishima Group.

Carinocarcinoides angustifrons

(Karasawa, 1993) comb. nov.

Figure 5.3

Varuna angustifrons Karasawa, 1993, p. 81, pl. 23, fig. 13;
Karasawa, 1997, p. 69, pl. 27, fig. 8.

Revised diagnosis.—*Carinocarcinoides* with rounded-quadrate carapace and with epigastric, protogastric, cardiac and epibranchial ridges.

Revised description.—Carapace roundly quadrate in outline, about as long as wide, widest at midlength. Orbitofrontal margin 0.75 carapace width. Front straight, occupying about 0.3 carapace width, with sharp lateral corners. Upper orbital margin wide, concave, rimmed, with small, forwardly directed outer orbital spine. Anterolateral margin gently convex, about 0.4 carapace width, with two small spines excluding outer orbital spine. Posterolateral margin also strongly convex, about 1.4 times as long as anterolateral margin. Posterior margin straight, about 0.4 carapace width.

Dorsal surface smooth, moderately vaulted transversely and weakly vaulted longitudinally. Regions somewhat distinct. Epigastric region with weak, transverse ridge on each side. Protogastric regions inflated with broad, transverse ridge interrupted by narrow anterior mesogastric process. Anterior mesogastric process poorly defined. Mesogastric region slightly convex. Cervical groove distinct, sinuous. Cardiac region gently inflated transversely, hexagonal in outline, bearing two nodes transversely arranged, with anterior transverse ridge. Intestinal region poorly defined. Hepatic region depressed. Branchiocardiac grooves shallow. Branchial regions convex; each epibranchial region inflated with broad ridge extending in convex-forward arc from mesogastric region to last anterolateral spine.

Discussion.—The present species was originally placed in *Varuna* H. Milne Edwards, 1852 in the family Grapsidae. However, the species is moved here from *Varuna* to

Carinocarcinoides on the basis of its inflated dorsal carapace with several ridges and three anterolateral spines. Members of *Varuna* have a flattened dorsal surface with a wider frontal margin and three broadly triangular anterolateral teeth.

Material examined.—MFM218501 (holotype) from KSM-2.

***Carinocarcinoides carinatus* sp. nov.**

Figure 5.1a–d, 5.2, 5.4

Diagnosis.—*Carinocarcinoides* with transversely hexagonal carapace and with anterior frontal, protogastric, urogastric, cardiac and epigastric ridges dorsally.

Etymology.—From Latin *carina* (= keel), in reference to dorsal ridges on the carapace.

Description.—Carapace transversely hexagonal in outline, length 0.8 its width, widest at anterolateral angle. Orbitofrontal margin occupying about 0.75 carapace width. Front nearly straight, about 0.4 carapace width, weakly protruded medially, with well developed ridge parallel to anterior margin and with sharply squared corners. Upper orbital margin concave, rimmed, with weak, central projection and broadly triangular, forwardly directed outer orbital spine. Inner suborbital spine sharp, projecting anteriorly, visible in dorsal view. Anterolateral margin strongly convex, about 0.35 carapace width, with two small, anterolaterally directed spines exclusive of outer orbital spine. Posterolateral margin also strongly convex, about 1.8 times as long as anterolateral margin. Posterior margin short, about 0.3 carapace width.

Dorsal surface smooth, moderately vaulted transversely and weakly vaulted longitudinally. Regions distinct. Protogastric region inflated with broad, arcuate ridge on each side. Anterior mesogastric process poorly defined. Mesogastric region slightly convex. Urogastric region with transverse ridge. Cervical groove well defined, sinuous. Cardiac region gently vaulted transversely, hexagonal in outline, bearing two nodes transversely arranged, with transverse ridge anteriorly. Intestinal region small, poorly defined. Hepatic region flattened. Branchiocardiac grooves fairly deep. Branchial regions convex; each epibranchial region most strongly inflated with broad ridge extending in convex-forward arc from mesogastric region to last anterolateral spine. Infraorbital region with weak, granulated ridge parallel to lower orbital margin. Pterygostomian region bearing finely granulated ridge below and parallel to pleural suture. Maxilliped 3 poorly preserved.

Thoracic sternum longer than wide, tapering anteriorly and posteriorly, occupying about 0.4 carapace width, widest at sternite 6. Sternites 1 and 2 fused, triangular. Sternite 3 twice as wide as long with shallow median depression; anterior margin weakly concave, posterior margin broadly V-shaped, lateral margin straight, converging anteriorly. Sternites 4–7 with blunt episternal projections. Sternite 4 about 1.5 times wider than long, narrower anteriorly, wider posteriorly; anterior and posterior margins broadly V-shaped, lateral margins convex. Sternite 5 wider than long, becoming narrower anteriorly; anterior margin broadly V-

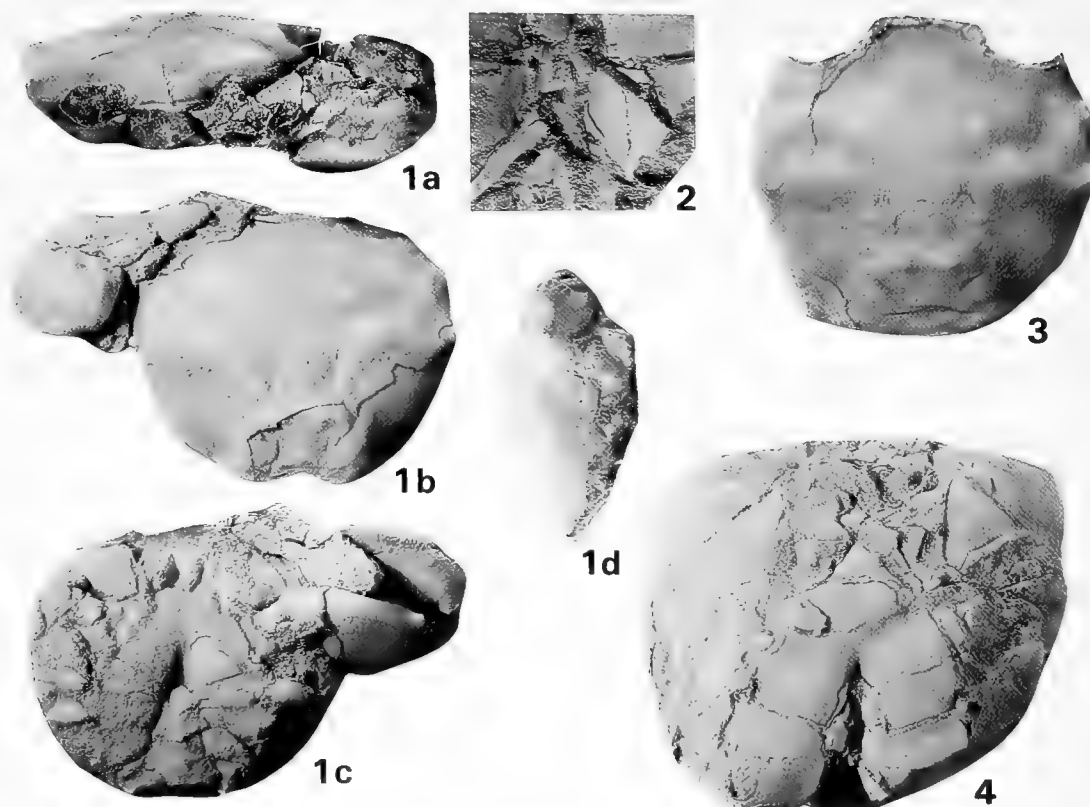


Figure 5. 1a-d. *Carinocarcinoides carinatus* gen. et sp. nov., MFM218513 (holotype), $\times 2.0$; 1a: carapace and left cheliped, frontal view; 1b: carapace and left cheliped, dorsal view; 1c: carapace, thoracic sternum, abdomen of male, and left cheliped, ventral view; 1d: carapace, lateral view. 3. *Carinocarcinoides angustifrons* (Karasawa, 1993) comb. nov., MFM218501 (holotype), carapace, $\times 2.5$, dorsal view. 2, 4. *Carinocarcinoides carinatus* gen. et sp. nov., MFM218514 (paratype), 2: pleopods, $\times 3.0$, ventral view; 4: carapace and thoracic sternum, $\times 1.5$, ventral view.

shaped, posterior margin sinuous, lateral margin convex. Sternites 6 and 7 wider than long, narrowing posteriorly; anterior and posterior margins sinuous, lateral margin convex. Sternite 8 directed strongly posterolaterally with weak lateral projections. Pleopods poorly preserved.

Abdomen of male narrow. Telson triangular, as long as wide at base. Somites 4–6 preserved, widest at posterior part of somite 4, with straight, anteriorly convergent lateral margins; somite 6 about as long as wide; somites 4 and 5 wider than long.

Left cheliped large, poorly preserved. Dorsal surface of dactylus and lateral surface of palm finely granulate. Lateral surface of carpus also finely granulate with finely granulated ridge parallel to proximal margin; dorsal margin with forwardly directed spine.

Discussion.—A transversely hexagonal carapace with transverse frontal and urogastric ridges readily distinguishes *C. carinatus* from *C. angustifrons*. In *C. carinatus* the carapace length occupies about 80 % of the width, while in *C. angustifrons* a roundly quadrate carapace is about as long

as wide.

Material examined.—MFM218513 (holotype) and 218514 (paratype) from KSM–9.

Subfamily Chasmocarcininae Serène, 1964
Genus ***Collinsius*** Karasawa, 1993

Type species.—*Collinsius simplex* Karasawa, 1993 by monotypy.

Geologic range.—Early Oligocene.

Revised diagnosis.—Carapace slightly wider than long, widest at posterolateral angle. Orbitofrontal margin occupying about half carapace width. Front narrow, bilobed, projecting anteriorly, with squared lateral corner. Upper orbital margin narrow, concave, rimmed, with broadly triangular outer orbital angle. Lateral margin rounded, divergent posteriorly. Posterior margin short, straight. Dorsal surface smooth, gently convex longitudinally and transversely. Epigastric region poorly defined. Cervical groove becoming obsolete in advance of hepatic region. Urogastric region

narrow, depressed. Cardiac region transversely convex. Intestinal region narrow. Branchiocardiac grooves well defined. Branchial regions inflated. Thoracic sternum wide, wider than long, widest at sternite 6. Sternite 8 of male with supplementary sternal plate. Abdomen of male narrow; somites 3–5 fused. Chelipeds unequal.

Discussion.—Karasawa (1993) originally placed the genus in the family Goneplacidae, but did not assign it to any known subfamily. Later, Karasawa (1997) assigned *Collinsius* to the subfamily Chasmocarcininae by recognising the presence of supplementary sternal plates of the thoracic sternite 8 in the male. The subfamily Chasmocarcininae comprises five extant genera, *Chasmocarcinus* Rathbun, 1898, *Camatopsis* Alcock and Anderson, 1899, *Chasmocarcinops* Alcock, 1900, *Hepthopelta* Alcock, 1899 and *Scalopidia* Stimpson, 1858, and the Eocene *Falconoplax* Van Straelen, 1933 (Davie and Guinot, 1996). Among these genera, *Collinsius* resembles *Chasmocarcinus*, *Hepthopelta* and *Falconoplax* in that abdominal somite 3 of the male fuses to somites 4 and 5. However, the genus differs from *Chasmocarcinus* by having a narrow front and lacking the posterolateral expansion of the carapace; *Hepthopelta* has a wider front and a strongly inflated dorsal carapace; the carapace of *Falconoplax* has well defined epibranchial regions, protogastric tubercles, deep branchiocardiac grooves and epibranchial ridges.

Collinsius is only known from the lower Oligocene Kishima Formation of Kyushu, Japan.

Collinsius simplex Karasawa, 1993

Figure 6.1–6.9

Collinsius simplex Karasawa, 1993, p. 73, pl. 21, figs. 3–8; Karasawa, 1997, p. 61, pl. 23, figs. 4–6, 8–10.

Revised description.—Carapace slightly wider than long, widest at posterolateral angle. Orbitofrontal margin occupying about half of carapace width. Front narrow, projecting anteriorly with shallow median depression dorsally; anterior margin nearly straight, interrupted by weak median notch with sharply squared lateral corner; lateral margin rimmed. Upper orbital margin concave, rimmed, occupying about 0.2 carapace width, with weak, central projection and broadly triangular outer orbital angle. Lateral margin rounded, divergent posteriorly. Posterior margin short, straight. Dorsal surface smooth, gently convex longitudinally and transversely. Epigastric region poorly defined, but visible. Protogastric region separated from anterior mesogastric process by shallow groove. Cervical groove becoming obsolete in advance of hepatic region. Urogastric region narrow, depressed. Cardiac region transversely hexagonal in outline, transversely convex. Intestinal region narrow. Branchiocardiac grooves well defined. Branchial regions inflated.

Thoracic sternum wide, wider than long, widest at sternite 6. Sternites 1 and 2 fused, narrow, broadly triangular in outline, with deep median depression. Sternite 3 about 0.3 as long as wide with median depression; anterior margin nearly straight, posterior margin broadly V-shaped, lateral margin straight, strongly converging anteriorly. Sternites 4–7 with

blunt episternal projections. Sternite 4 about 0.4 times longer than wide, narrower anteriorly, wider posteriorly; anterior and posterior margins broadly V-shaped; lateral margins convex. Sternite 5 wider than long, narrower anteriorly, wider posteriorly; anterior margin broadly V-shaped, posterior margin sinuous, lateral margin convex. Sternite 6 wider than long; anterior and posterior margins sinuous, lateral margin convex. Sternite 7 wider than long, wider anteriorly, narrower posteriorly; anterior and posterior margins sinuous, lateral margin convex. Sternite 8 wider than long, wider anteriorly, narrower posteriorly, directed posterolaterally; supplementary sternal plate developed in male; shallow, transverse groove in female surface.

Abdomen of male narrow. Telson triangular, slightly longer than wide at base. Somite 6 wider than long with straight, anteriorly convergent lateral margins. Somites 3–5 fused, wider than long, widest at base, with slightly concave, anteriorly convergent lateral margins; posterior lateral expansions covering mesial ends of supplementary plates. Somite 2 narrow. Somite 1 unknown. Telson of female abdomen rounded, wider than long at base. Somites 1–6 narrow, much wider than long, widest at somite 3, longest at somite 6.

Chelipeds unequal. Fixed finger short on major cheliped; palm with smooth, inflated lateral surface. Dactylus elongate on minor cheliped, curving ventrally, with acutely pointed tip; fixed finger also elongate, about as long as dactylus, occupying about half of propodus length, slightly deflexed ventrally, with acutely pointed tip; palm longer than high, distal margin much wider than proximal margin, with smooth, inflated lateral surface.

Pereiopods 1–4 of female poorly preserved. Propodi of pereiopods 2–4 elongate, cylindrical in cross section. Coxa and ischium fused to basis short.

Discussion.—As for the genus.

Material examined.—MFM218502 (holotype), 218503 (paratype), and 218601–218610 from KSM-2; MFM218505 (paratype), 218506 (paratype), and 218613–218620 from KSM-4; MFM218504 (paratype), 218621–218630, 218640, 218641 from KSM-5; MFM218612 from KSM-3; MFM 218642, 218643 and 218644 from KSM-6; referred specimens from KSM-7, 8, 9, 10, 11.

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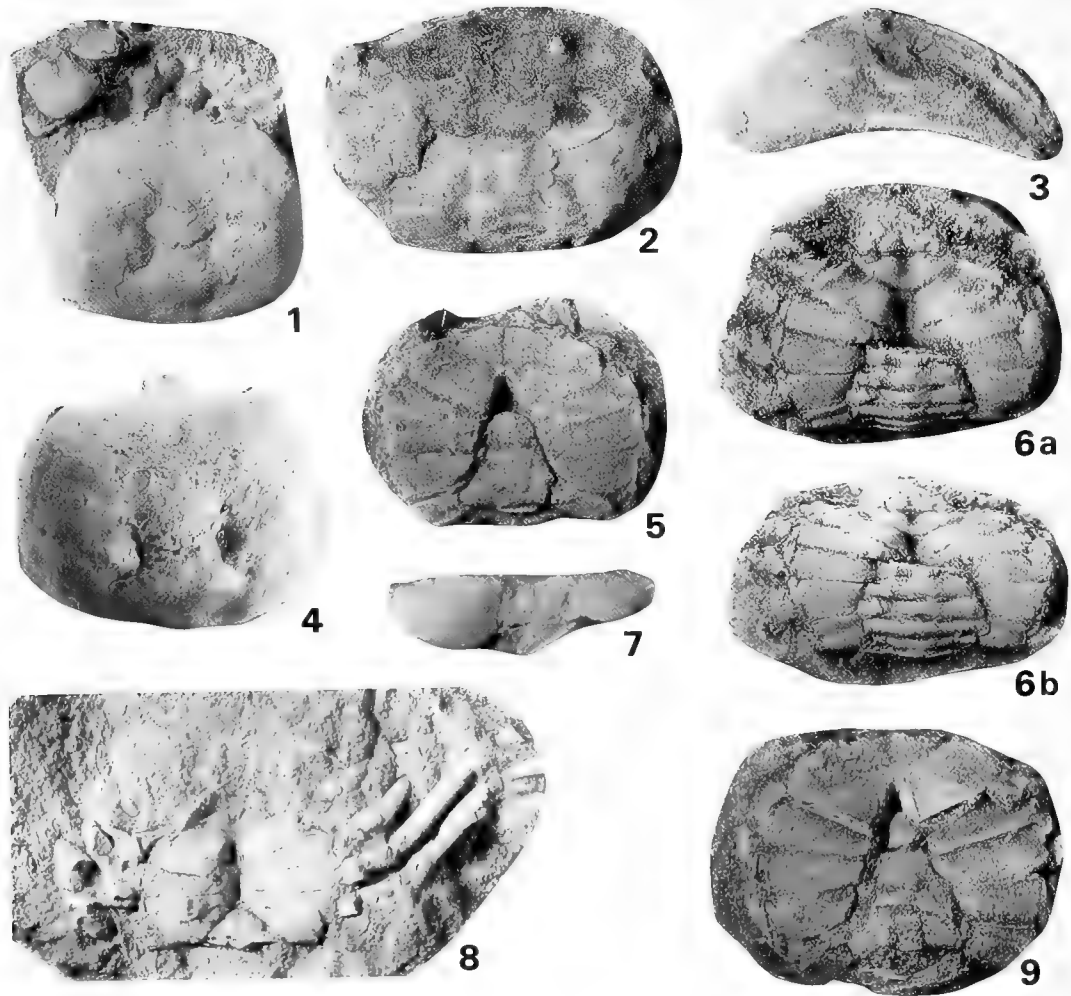


Figure 6. 1–9. *Collinsius simplex* Karasawa, 1993; 1: MFM218502 (holotype), carapace and left cheliped, $\times 3.0$, dorsal view; 2: MFM218642, thoracic sternum and abdomen of female, $\times 3.0$, ventral view; 3: MFM218640, right cheliped, $\times 3.0$, lateral view; 4: MFM218504 (paratype), carapace, $\times 4.0$, dorsal view; 5: MFM218505 (paratype), thoracic sternum and abdomen of male, $\times 3.0$, ventral view; 6a, b: MFM218643, thoracic sternum and abdomen of female, $\times 3.0$, ventral view; 7: MFM218503 (paratype), both chelipeds, $\times 2.5$, lateral view; 8: MFM218641, thoracic sternum and pereopods of female, $\times 3.0$, ventral view; 9: MFM218644, thoracic sternum and abdomen of male, $\times 3.0$, ventral view.

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New cephalopod material from the Bashkirian (Middle Carboniferous) of the Ichinotani Formation, Central Japan

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Abstract. Three Bashkirian (Middle Carboniferous) species of orthocerid cephalopods, the orthoceratid *Hidamichelinoceras bandoi* gen. et sp. nov. and the pseudorthoceratids *Mooreoceras* sp. and *Adnatoceras ichinotaniense* Niko and Hamada, 1987, are described (or redescribed) from the Ichinotani Formation, Central Japan based on new material. The siphuncular structure of *Hidamichelinoceras* is shared with *Michelinoceras*, but this new genus is characterized by its broadly cone-shaped initial camera and rapid shell expansion. The discovery of *Mooreoceras*, which previously had been known only from the Hikoroichi Formation in Japan, supports a paleobiogeographic link between the Fukui and southern Kitakami areas in the Carboniferous. The apical shell diagnosis of *Adnatoceras ichinotaniense* is added.

Key words: Bashkirian (Middle Carboniferous), *Hidamichelinoceras* gen. nov., Ichinotani Formation, Orthocerida.

Introduction

Recent research on Far Eastern Carboniferous orthocerids and bactritids has shown that at least two isolated faunal provinces were present through the period in the area, i. e., the Taishaku-Akiyoshi-South China Province with the *Bogoslovskya* and *Bactrites* lineage (Niko *et al.*, 1987, 1991, 1995, 1997; Niko and Ozawa, 1997) and the southern Kitakami-Fukui Province with the *Adnatoceras* lineage (Niko and Hamada, 1987; Niko, 1990). Nevertheless, our knowledge of Carboniferous orthoconic cephalopods is too limited to permit detailed paleobiogeographic reconstruction. Descriptive works are still critical also for providing phylogenetic information about these groups. As an additional account of orthocerid cephalopods in the Fukui area, Central Japan, this work documents a new collection from the Bashkirian (Middle Carboniferous) limestone of the Ichinotani Formation. Details of the geologic setting and stratigraphic position of the collection have already been given by Niko and Hamada (1987).

The abbreviation UMUT for the repository stands for the University Museum of the University of Tokyo.

Systematic paleontology

Order Orthocerida Kuhn, 1940
Superfamily Orthocerataceae M'Coy, 1844
Family Orthoceratidae M'Coy, 1844
Subfamily Michelinoceratinae Flower, 1945
Genus *Hidamichelinoceras* gen. nov.

Type species.—*Hidamichelinoceras bandoi* sp. nov., by monotypy.

Diagnosis.—Orthoconic michelinoceratinid with rapid shell expansion, 9°–13° in angle, for subfamily, circular cross section, and probably endogastric early juvenile portion; shell surface ornamented by transverse lirae; initial camera broadly cone-shaped with rounded apex, shallow; early siphuncle central then becoming subcentral in position; septal necks very long and orthochoanitic, forming very wide septal foramen; cameral deposits weakly developed, episepal-mural and hyposeptal; auxiliary deposits absent.

Etymology.—The generic name is derived from Hida, which is a historic provincial name of the type locality, and *Michelinoceras*.

Hidamichelinoceras bandoi sp. nov.

Figures 1.1–1.6, 2.1

Diagnosis.—Same as for the genus.

Description.—Based on single incomplete phragmocone of orthoconic shell with circular cross section; early juvenile shell indicates probable endogastric curvature; shell expansion rapid as for subfamily, its angle approximately 13° apically, then decreases to approximately 9° adorally; diameter of adoral shell attains 6.2 mm. Surface ornamentation consists of transverse and somewhat distant lirae forming weak sinuations. Sutures not observed, but obvious obliquity not recognized in dorsoventral section. Initial camera broadly cone-shaped with rounded apex, shallow and relatively small with 0.9 mm+ (slightly deformed) in maximum diameter and 0.3 mm in length between both apexes of initial and second camerae; cameral length abruptly increases in following camerae, then re-shortened adorally; maximum diameter/length ratios of adoral camerae range from 1.7 to 2.2; septal curvature moderate to relatively deep in seven apical septa, then becomes shallower in adoral septa. Siphuncular position nearly central in early juvenile shell, then slightly shifts in ventral direction, subcentral; minimum distance of central axis of siphuncle from shell surface versus shell diameter decreases to 0.4; caecum weakly inflated; siphuncle consists of orthochoanitic septal necks and nearly cylindrical connecting rings in second to seventh camerae; connecting rings missing in adoral camerae where septal necks are orthochoanitic, very long, 0.65–0.79 mm in length, attaining 0.3 in ratio of septal neck length/cameral length; diameters of septal necks are 0.61–0.71 mm; septal foramen cylindrical, very wide for subfamily, 0.52–0.63 mm in diameter; ratio of septal neck diameter to corresponding dorsoventral shell diameter attains 0.13. Cameral deposits weakly developed, restricted to apical 10 camerae, episeptal-mural and hyposeptal, slightly thicker in venter than dorsum; circumsiphuncular ridges of episeptal and hyposeptal deposits partly extend onto ventral side of connecting rings and septal necks, respectively. Endosiphuncular deposits, including auxiliary ones, are absent.

Discussion.—The siphuncular structure of *Hidamichelino-ceras bandoi* gen. et sp. nov. suggests a close relationship to the widespread genus *Michelinoceras* (Foerste, 1932; type species *Orthoceras michelini* Barrande, 1866). The most important distinctive feature is the morphology of the initial camera. In contrast to the broadly cone-shaped initial camera of this new genus, the longitudinally elongated bulbous form of the type species of *Michelinoceras* was confirmed by Ristedt (1968, pl. 1, fig. 1). The rapid shell expansion (9° – 13° in angle) of *Hidamichelino-ceras* in comparison with the much slenderer shell shape of *Michelinoceras* (1° – 2° in angle of shell expansion of *M. michelini*) is also regarded as enough to be of generic significance. *Hidamichelino-ceras* differs from the Devonian to Carboniferous genus *Bogoslovskya* (Zhuravleva, 1978; type species, *B. perspicua* Zhuravleva, 1978) in having a less eccentric siphuncular position with a wider septal foramen and in lacking auxiliary deposits. The Triassic genus *Trematoceras* (Eichwald, 1851, not seen by the author; its generic diagnosis, including apical shell morphology, comes from citation by Schindewolf, 1933; type species, *Orthoceratites elegans* Münster, 1841) has a cone-shaped initial camera but the shape of the septal necks of *Hidamichelino-ceras* is

quite unlike that of *Trematoceras*, whose septal necks are very short and suborthochoanitic. In addition, the cameral deposits of *Trematoceras* are characterized by the prominent lamellae. The circular shell cross section of *Hidamichelino-ceras* clearly separates it from the Devonian genus *Arkonoceras* (Flower, 1945; type species, *Orthoceras arkonense* Whiteaves, 1898), which has a much slenderer shell characterized by its subquadrangular cross section.

The Ordovician genus *Sinoceras* (Shimizu and Obata, 1935; type species, *Orthoceras chinense* Foord, 1888) was erroneously assigned to the Michelinoceratinae (e.g., Sweet, 1964) owing to its orthoconic shell shape and its *Michelinoceras*-like very long septal necks indicating orthochoanitic forms. However, the enveloping cameral-endosiphuncular deposits on the septal neck and on both the adoral and apical surfaces of the septum, recognized in the type species of *Sinoceras* in Woodward's (1856, pl. 6, fig. 1) illustration, undoubtedly place *Sinoceras* in the family Lituitidae within the order Tarphycerida.

Material examined and occurrence.—Holotype, UMUT PM 27849, 28.0 mm in length from the uppermost part of the Lower Member, Ichinotani Formation.

Etymology.—The specific name refers to the late Dr. Yuji Bando, in recognition of his contributions to the study of fossil cephalopods.

Superfamily Pseudorthocerataceae Flower
and Caster, 1935

Family Pseudorthoceratidae Flower and Caster, 1935
Subfamily Pseudorthoceratinae Flower and Caster, 1935
Genus *Mooreoceras* Miller, Dunbar and Condra, 1933

Type species.—*Mooreoceras normale* Miller, Dunbar and Condra, 1933.

Mooreoceras sp.

Figures 1.7–1.9, 2.7

Description.—Orthoconic phragmocone with gradual shell expansion and dorsoventrally depressed, oval cross section; diameter of apical end is 5.2 mm in dorsoventral direction and 5.8 mm in lateral direction, giving a form ratio of approximately 1.1. Surface ornamentation absent. Sutures transverse, nearly straight, or strongly oblique in rare cases; septal curvature shallow. Cameral length moderate for genus, cameral ratios of maximum dorsoventral diameter/maximum length are 0.2–0.4. Siphuncle subcentral, consists of cyrtchoanitic septal necks and subcylindrical connecting rings whose inflation is weak for genus. Cameral deposits not detected. Endosiphuncular deposits form annulosiphonate rings.

Discussion.—Although this species is known from a single specimen of a probable juvenile shell judging from the relatively weak inflation of the connecting rings, the oval cross section of the shell, subcentral siphuncular position with the cyrtchoanitic septal necks, annulosiphonate rings formed of endosiphuncular deposits and the lack of cameral deposits warrant generic assignment to *Mooreoceras*. Unsuccessful attempts to make a well-oriented thin section preclude a specific determination.

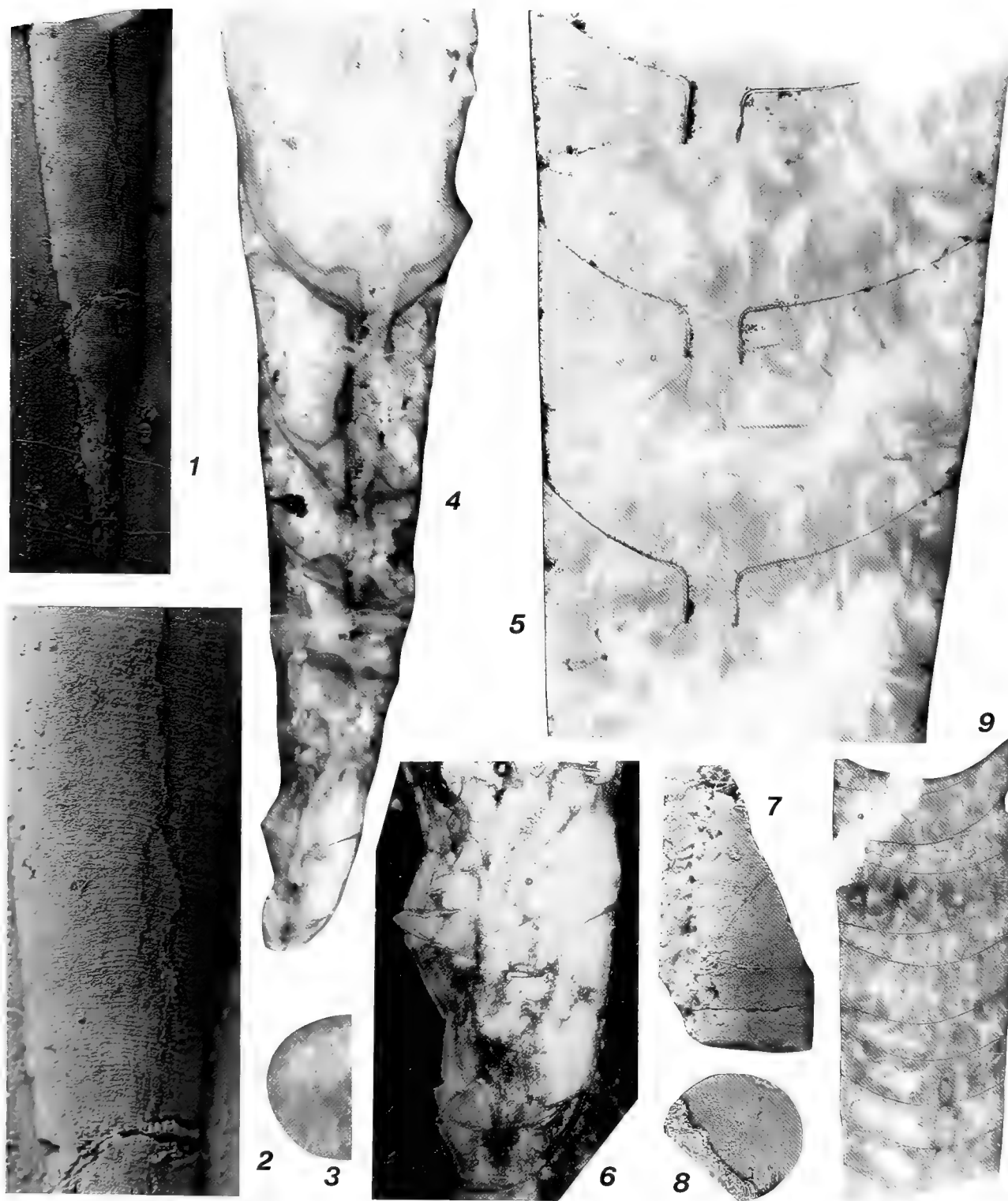


Figure 1. 1-6. *Hidamichelinoceras bandoi* gen. et sp. nov., holotype, UMUT PM 27849. 1: Lateral view of silicone rubber cast, venter on right, $\times 4$; 2: Details of shell surface, showing ornamentation of transverse lirae, $\times 8$; 3: Polished cross section, venter down, $\times 4$; 4: Longitudinal thin section of apical shell, venter on left, slightly deformed, $\times 14$; 5: Longitudinal thin section of adoral shell, venter on left, $\times 14$; 6: Details of the three most apical camerae, note cone-shaped initial camera, ventral shell slightly deformed, $\times 30$. 7-9. *Mooreoceras* sp., UMUT PM 27850. 7: Dorsal view, $\times 4$; 8: Septal view of apical end, venter down, $\times 4$; 9: Longitudinal thin section, venter on right, $\times 5$.

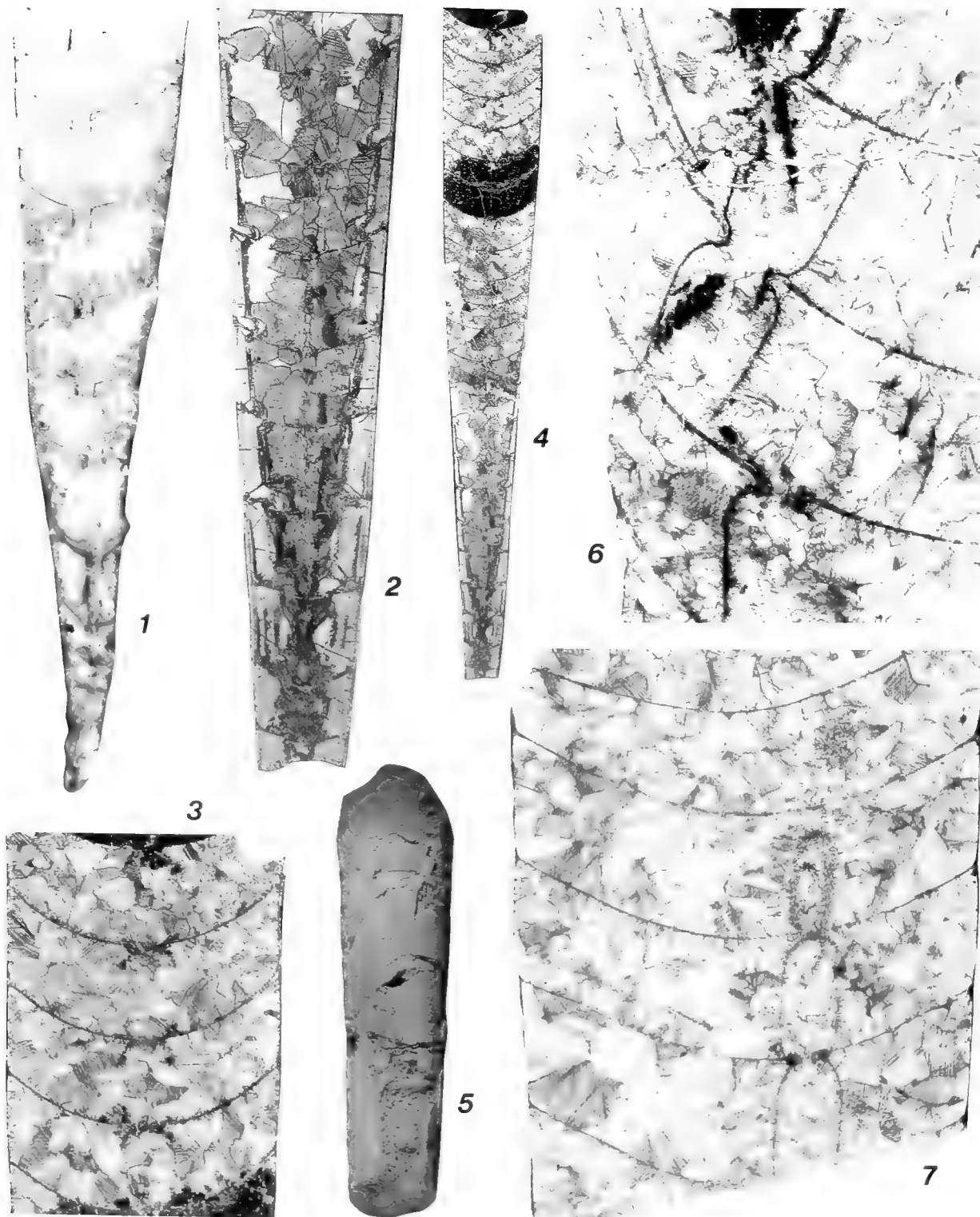


Figure 2. 1. *Hidamichelinoceras bandoi* gen. et sp. nov., holotype, UMUT PM 27849, longitudinal thin section, venter on left, $\times 5$. 2–6. *Adnatoceras ichinotaniense* Niko and Hamada, 1987. 2–4: UMUT PM 27852; 2: Longitudinal thin section of apical shell, venter on right, $\times 14$; 3: Longitudinal thin section of adoral shell, venter on right, $\times 14$; 4: Longitudinal thin section, venter on right, $\times 5$; 5, 6: UMUT PM 27851; 5: Ventral view, $\times 2$; 6: Longitudinal thin section, details of adoral siphuncular structure, venter on left, $\times 14$. 7. *Mooreoceras* sp., UMUT PM 27850, longitudinal thin section, venter on right, showing siphuncular structure, $\times 14$.

Previously, this genus had been represented in Japan solely by *Mooreoceras kinnoi* Niko, 1990, from the Visean (Early Carboniferous) of the Hikoroichi Formation in the southern Kitakami area, Northeast Japan. The present discovery of *Mooreoceras* sp. from the Fukuji area supports a paleobiogeographic link in the Carboniferous between the Fukuji and southern Kitakami areas, of which the similarity has also been suggested by the common occurrence of *Adnatoceras* in both areas.

Material examined and occurrence.—Single incomplete phragmocone, UMUT PM 27850, 15.0 mm in length. Stratigraphic horizon is identical with *Hidamichelinoceras bandoi*.

Subfamily Spyroceratinae Shimizu and Obata, 1935
Genus ***Adnatoceras*** Flower, 1939

Type species.—*Orthoceras spissum* Hall, 1879.

Adnatoceras ichinotaniense Niko and Hamada, 1987

Figure 2.2–2.6

Adnatoceras ichinotaniensis Niko and Hamada, 1987, p. 225, 227, figs. 3–1–6.

Adnatoceras ichinotaniense Niko and Hamada. Niko, 1990, p. 557; Kamiya and Niko, 1992, fig. 1–E.

Additional diagnosis.—Early siphuncle central in position with suborthochoanitic septal necks and cylindrical connecting rings. See Niko and Hamada (1987, p. 225) for diagnosis of adult shell.

Description.—Orthoconic shells with dorsoventrally depressed subcircular cross section up to nearly 4 mm in diameter and with a mean form ratio of approximately 1.1, then circular cross section attaining 9.1 mm in diameter; shell expansion moderate for genus, its angle approximately 4° in apical shell, then decreases to 2°–3° in adoral shell. Surface ornamentation absent; ventral wall slightly thicker than dorsal wall. Sutures straight, slightly oblique with approximately 5° to rectangular direction of shell axis, toward aperture on venter; septa relatively shallow; cameral length moderate to relatively short for genus; maximum width/length ratio of apical camerae ranges from 1.3 to 2.0, and ratio increases to 2.9–5.8 with 3.9 mean in adoral camerae. Early siphuncle central in position, composed of very short suborthochoanitic septal necks, 0.13 mm in length for a well-preserved one, and cylindrical connecting rings having weak constrictions at septal foramen; siphuncular position shifts towards a ventral one as shell grows, subcentral; ratio of minimum distance of central axis of the most adoral siphuncle from shell surface per shell diameter decreases to 0.3, where septal necks are asymmetrical, suborthochoanitic to cyrtchoanitic on dorsal side, with a length of 0.31 mm, and strongly recurved cyrtchoanitic on ventral side, with a length of 0.22 mm; adoral connecting rings subcylindrical, nearly parallel-sided and abruptly constricted at septal foramen; maximum diameter/length ratio of adoral siphuncle 0.5–0.7; adnation area very wide for family. Cameral deposits usually episeptal-mural and hyposeptal, but the latter are absent in some camerae, thicker in venter than dorsum.

Endosiphuncular parietal deposits restricted on ventral siphuncular wall, thin, not fused. Adoral camerae lack both cameral and endosiphuncular deposits.

Discussion.—The description above is the same as in Niko and Hamada (1987) except that the apical shell morphology and most adoral siphuncular structures are added based on new specimens. The weaker cameral and endosiphuncular deposits of one specimen (UMUT PM 27852), compared to the holotype, probably result from its immaturity.

Material examined and occurrence.—Holotype, UMUT PM 18068; paratype, UMUT PM 18069. In addition, two newly collected incomplete phragmocones were examined: UMUT PM 27851, which includes more of the adoral shell than the type specimens, 38.3 mm in length, and UMUT PM 27852, which represents more of the apical shell than the type specimens, 23.0 mm in length. Stratigraphic horizon is identical with *Hidamichelinoceras bandoi*.

Acknowledgments

The author is grateful to Takashi Hamada for his helpful comments in the early stages of this study and to Hisayoshi Igo who provided locality information for the present cephalopods. Toshiaki Kamiya collected most of the specimens utilized in this study.

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Further notes on the turrilitid ammonoids from Hokkaido— Part 1 (Studies of the Cretaceous ammonites from Hokkaido and Sakhalin—LXXXIX)

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Abstract. This paper contains the descriptions of *Ostlingoceras* (*Ostlingoceras*) *bechei* (Sharpe, 1857), *O. (O.)* aff. *bechei*, and *Neostlingoceras carcitanense* (Matheron, 1842), all from the lower Cenomanian of the Mikasa and Kotanbetsu areas; also those of two new species *Neostlingoceras asiaticum* and *N. cobbani* from the middle Cenomanian of the Mikasa area. A new genus *Hypostlingoceras* is established, with descriptions of two new species, *H. japonicum* (type species) and *H. mikasaense*, from the lower Cenomanian of the same area.

Key words: *Carthaginites*, Cenomanian, *Hypostlingoceras*, *Neostlingoceras*, *Ostlingoceras*, Turrilitidae

Introduction

Recently ten species of *Mariella* and a few species of *Mesoturrilites*, *Hypoturrilites* and *Pseudhelicoceras* from the Cretaceous of Hokkaido have been described (Matsumoto *et al.*, 1999; Matsumoto and Kawashita, 1999; Matsumoto and Kijima, 2000; Matsumoto and Inoma, 1999; Matsumoto *et al.*, 2000). Sources of the material for these investigations are collections from the upper Albian and lower Cenomanian of the Soeushinai area of northwestern Hokkaido and the Shuparo and Hobetsu areas of central Hokkaido.

In this and succeeding papers additional species of the Turrilitidae are to be described. The material for this paper depends mainly on the collections from the celebrated Ikushunbetsu Valley of the Mikasa area. For a general account of the stratigraphy and the locality data readers may refer to Matsumoto (1991, p. 3–5; 21–24). Supplementary notes may be added to the particular cases concerned.

The purpose of our series of papers is to present precisely the systematic descriptions of the turrilitid ammonoids from the Cretaceous Yezo Group of Hokkaido, with confirmation or revision of previously known species and also establishment of new taxa. The described species could be useful for biostratigraphic subdivision and interregional correlation. As the faunal characteristics of the subdivided units of the Albian and the Cenomanian in the North Pacific region become clearer, the results could improve the knowledge of its palaeogeography and palaeoenvironments.

Repository.—The specimens described in this paper are to be stored in the Kyushu University Museum, Fukuoka, 812–8581, Japan, which is indicated by the letters GK at the head of a register number. To each specimen collected by T. T. a personal number was provisionally given. This numbering was set in accordance with the date of his field work. Although not official register numbers, they should not be ignored, because they are written clearly in red ink on each specimen and because they are tied to his field notes and will enable readers to get useful information. In this paper such numbers are indicated in brackets, as for instance, GK. H8531 [= previous S. 37·7·17] (Figure 1 D–F). Herein S. means *Showa*, a reign style in Japan and S. 37 = 1962.

A few specimens which were housed in the Geological Collections, Faculty of Culture and Education, Saga University, Saga, 840–8502, Japan (abbreviated as GS), are transferred to GK.

Systematic descriptions

Order Ammonoidea Zittel, 1884
Suborder Ancyloceratina Wiedmann, 1966
Superfamily Turrilitaceae Gill, 1871
Family Turrilitidae Gill, 1871
Genus *Ostlingoceras* Hyatt, 1900
Subgenus *Ostlingoceras* (*Ostlingoceras*) Hyatt, 1900

Type species.—*Turrilites puzosianus* d'Orbigny, 1842 (p. 587, pl. 143, figs. 1, 2) by original designation (Hyatt, 1900,

p. 587).

Diagnosis.—See Wright and Kennedy, 1996, p. 320.

Remarks.—Wright and Kennedy (1996, p. 320) treated *Parostlingoceras* Breistroffer (1953, p. 1350) as a subgenus of *Ostlingoceras*. No example of *O. (Parostlingoceras)* has been found in Hokkaido. In addition to *O. (O.) puzosianum* ten species were assigned to *O. (Ostlingoceras)* by Wright and Kennedy (1996, p. 321). Moreover, *Turrilites* cf. *colcanapi* of Pervinqui re (1910, p. 50, pl. 14, fig. 4) from Algeria was revised to *O. (O.) collignoni* Wright and Kennedy (1996, p. 340, text-fig. 138E), although it deviates from the normal species of *O. (Ostlingoceras)* in its larger apical angle.

The available material of *O. (Ostlingoceras)* from Hokkaido is not numerous but fairly good in showing the characters that enable us to define more clearly previously named species. There are a few other indefinite taxa which are temporarily placed in this subgenus. One of them is described in this paper.

***Ostlingoceras (Ostlingoceras) bechei* (Sharpe, 1857)**

Figures 1A–C, D–F; 2A, B

Turrilites bechei Sharpe, 1857, p. 66, pl. 26, fig. 13 [as *bechii* on p.

66]

Ostlingoceras bechei (Sharpe, 1857). Wright and Wright, 1951, p. 18; Marcinowski, 1970, p. 435, pl. 3, fig. 5; Kennedy, 1971, p. 25 (*pars*), pl. 8, figs. 9, 13.

Ostlingoceras (Ostlingoceras) bechii (Sharpe, 1857). Atabekian, 1985, p. 50, pl. 14, fig. 6.

Ostlingoceras (Ostlingoceras) bechei (Sharpe, 1857). Wright and Kennedy, 1996, p. 321, pl. 96, figs. 6, 14–16, 18, 23.

Name of the species.—Two names have been used for this single species since Sharpe's (1857) original paper: *Turrilites Bechii* in the heading of the description (p. 66) and *Turrilites Bechei* in the explanation to plate 26, fig. 13a, b. Sharpe noted that the specimen was found by Sir H. T. de la Beche, and that it was named in his memory. We agree with Wright and Wright (1951, p. 18) in regarding *T. Bechii* as an obvious misprint for *T. Bechei*.

Holotype.—By monotypy, BMNH 88, the original of Sharpe, 1857, pl. 26, fig. 13, from the 'Cenomanian Limestone' near Lyme Regis, Devon (southern England).

Material.—GK.H8529 (Figure 1A, B, C), found by Tamotsu Omori near Loc. Ik1065b of the Shimo-ichino-sawa, a tributary of the River Ikushunbetsu; GK. H1381 (not figured), obtained in 1955 by T. M. at Loc. Ik1065b; GK.H8531 [previous

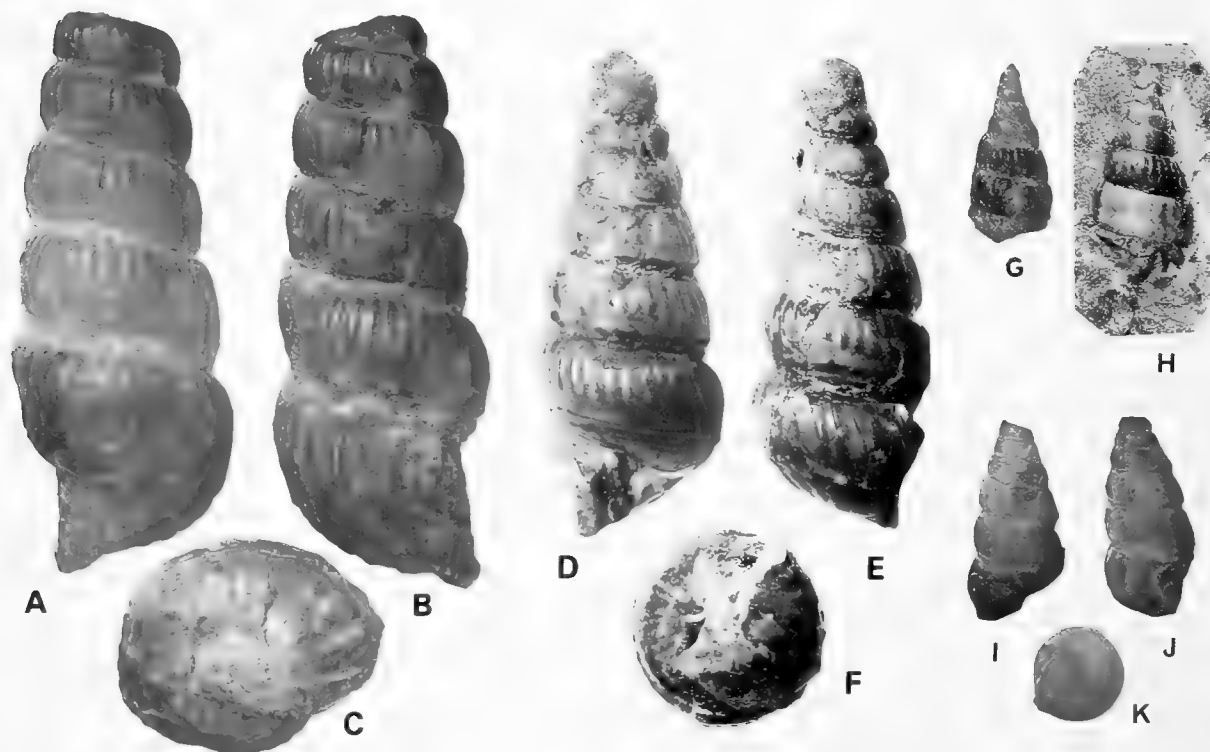


Figure 1. A–C, D–F. *Ostlingoceras (Ostlingoceras) bechei* (Sharpe, 1857). Two lateral (A and B, 180° apart) and basal (C) views of GK.H8529; similar views (D, E, F) of GK. H8531. G–H, I–K. *Ostlingoceras* aff. *bechei* (Sharpe, 1857). Extracted (G) and undeveloped (H) states of GK. H8530; two lateral (I, J) and basal (K) views of GK. H8555. All figures are $\times 2$, except for H ($\times 2.5$). Photos courtesy of M. Noda (D–F, H) and T. Nishida (others).

Table 1. Measurements of *Ostlingoceras* (*O.*) *bechei* (Sharpe).

| Specimen | NW | Hp | Ht | D | ap | h | d | h/d | R | r/h |
|-----------|----|------|------|------|-----|------|------|------|----|-----|
| GK. H8529 | 5 | 38.0 | 58.0 | 17.5 | 20° | 7.4 | 13.8 | 0.54 | 32 | 6–7 |
| GK. H8531 | 5 | 27.0 | 40.0 | 12.5 | 23° | 6.1 | 11.5 | 0.53 | 30 | 6 |
| BMNH88 | 4 | 50.0 | 75.0 | 29.8 | 20° | 11.5 | 21.5 | 0.53 | — | 7 |

NW = number of the preserved whorls, Hp = total height of the preserved whorls, Ht = total shell height from the preserved last whorl to the estimated apex, D = diameter of the preserved last whorl, ap = estimated apical angle, h = height of an exposed outer face [= flank] of a late whorl, d = diameter of the same whorl, R = number of ribs on the same whorl, r/h = number of ribs in the interval equal to h. Linear dimension is in mm.

S. 37·7·17] (Figure 1D, E, F), collected by T. T. in 1962 at a locality on the Onkonosawa, a branch of the River Ponbetsu, which is a major tributary of the River Ikushunbetsu.

Description.—The two illustrated specimens preserve five whorls but are dissimilar in size. Their dimensions are shown in Table 1. As the youngest part is lacking, the apical angle is estimated from the preserved part. It is fairly low but seems to vary to some extent between individuals (20°–23°).

The shell is turreted, sinistral, and the whorls are tightly in contact. The outer exposed whorl face is rounded, and its main part (= flank) is gently inflated and has a weak shoulder on its upper margin. Transverse ribs are numerous, somewhat prorsiradate, and moderately distinct. They are much weakened at (or interrupted by) a shallowly concave, narrow spiral zone in the lower part of the flank. They may be faintly swollen above this zone, showing sinuous curvature. Still lower, parallel to the lower whorl seam, there are two rows of spirally elongated tubercles, that correspond in number to the transverse ribs. The two rows tend to form narrow ridges, with an intervening, narrow groove between them. The lower ridge runs along the lower whorl seam. In other words it forms the outer outline of the basal surface, where the ribs extend to run with an anteriorly convex curvature to the narrow umbilicus. On the marginal part of the basal surface close to the second row of clavate tubercles there is another (i. e., fourth) row of small tubercles resting on the basal ribs.

The number of ribs seems to vary to some extent with growth and also between individuals. Where the shelly

layer is preserved the ribs are more distinct than on the internal mould.

In the preserved last part of GK. H8529, the largest specimen of the three, a few ribs tend to strengthen and curve more markedly than the other ones (Figure 1B, C). This could be inferred as flaring near the peristome, although the interpretation is uncertain.

Septal sutures are exposed on some parts of the flank, showing a fairly broad E–L saddle, L, and a narrower L–U saddle. These elements show minor incisions (Figure 2).

Comparison.—The specimens from Hokkaido are essentially similar to the holotype and other specimens from the 'Lower Chalk'. GK.H8529 surprisingly resembles the partly restored illustration of the holotype (Sharpe, 1857, pl. 26, fig. 13). Actually the holotype was in part enclosed by rock matrix, when one of us (T. M.) examined it at the Natural History Museum, London. Its characters are, however, well expressed by Sharpe's figure. The differences from the two illustrated specimens from Hokkaido are in the somewhat larger size and more delicate ribbing of the holotype. As the shelly layer is not preserved in the British specimen and as the number of ribs tend to increase with growth, the above differences are quite natural and would not invalidate the identification.

Discussion.—As described above, GK. H8529 may be almost adult, whereas the holotype, despite its larger shell, does not show the feature that should occur near the adult apertural end. This may suggest a difference in size. Wright and Kennedy (1996) pointed out the presence of size dimorphs in many species of the Turrititidae, although they did not discuss this problem with respect to *O.* (*O.*) *bechei*.

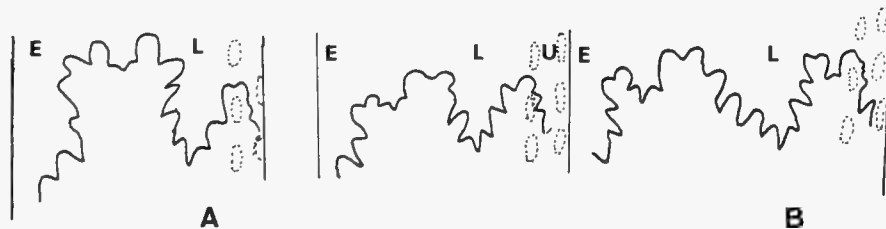


Figure 2. A, B. *Ostlingoceras bechei* (Sharpe, 1857). A: External suture on the-whorl flank of GK. H8531 at h = 4.5 mm. Figure is about $\times 7.5$. B: Ditto on the flank of successive whorls of GK. H8529 at h = 4.5 mm and 6.0 mm. Figure is about $\times 7$. Straight line: whorl seam, dotted line: tubercles; E: external lobe; L: lateral lobe; U: umbilical lobe. Drawing by T. M.

Table 2. Measurements of *Ostlingoceras* (*O.*) aff. *bechei* (Sharpe).

| Specimen | NW | Hp | Ht | D | ap | h | d | h/d | R | r/h |
|-----------|----|------|------|-----|-----|-----|-----|------|----|-----|
| GK. H8530 | 6 | 12.0 | 13.3 | 5.5 | 30° | 2.2 | 5.0 | 0.44 | 25 | 4-5 |
| GK. H8537 | 5 | 13.3 | 16.5 | 6.2 | 30° | 3.0 | 6.2 | 0.48 | 27 | 5 |

Legend as for Table 1.

In fact, the available specimens are not numerous enough to determine whether the size difference mentioned above is an indication of individual variation or implies dimorphism. The question is left for further investigation.

Occurrence.—As for material. On the basis of the location, lithology and associated species, the described three specimens came from the lower part of the Member IIb of the Mikasa Formation and are of early Cenomanian age.

Distribution.—*Ostlingoceras* (*O.*) *bechei* has been reported to occur in the lower Cenomanian of England, Poland and Azerbaijan (see Wright and Kennedy, 1996, p. 322). Its occurrence in Hokkaido of the North Pacific region suggests a more extensive distribution of this species.

***Ostlingoceras* (*Ostlingoceras*) aff. *bechei* (Sharpe, 1857)**

Figure 1G, H; I-K

Material.—Two small specimens: GK.H8530 (Figure 1G, H) collected by T. M. at Loc. Ik1065b of the Shimo-ichino-sawa, a tributary of the River Ikkushunbetsu; GK. H8555 [= previous GS.G058] (Figure 1I, J, K) collected by Tamio Nishida and T. M. at Loc. R735 pl in the upper reaches of the River Oku-futamata, a branch of the River Kotanbetsu (see Nishida *et al.*, 1993, fig. 1 for the location). The second specimen is probably derived from the upper part of the lower Cenomanian on the basis of its location and associated *Inoceramus* cf. *virgatus* Schlüter.

Description.—These two specimens are generally similar to the typical specimens of *Ostlingoceras* (*O.*) *bechei* (Sharpe, 1857) described above, but the young part, at the same size as the former, is lacking or poorly preserved in the latter. As is shown in Table 2, the estimated apical angle is somewhat larger and the ribs are less numerous and seem to be relatively coarser and shorter in the former in comparison with the latter. Moreover, the preserved earliest whorl (diameter = 1.3 mm in GK. H8530) shows an inflated flank. Tentatively, we call this taxon *Ostlingoceras* (*O.*) aff. *bechei* (Sharpe), although the above difference might imply a change with growth in *O.* (*O.*) *bechei*. It seems to resemble the taxon from Germany which was described under '*O.* (*O.*) aff. *bechei*' by Lehmann (1998, p. 37, without figure), but as we have not examined the actual specimen, we hesitate to confirm the identity.

Genus ***Neostlingoceras*** Klinger and Kennedy, 1978

Type species.—*Turrillites carcitanensis* Matheron, 1842 (p. 267, pl. 41, fig. 4) by original designation (Klinger and Kennedy, 1978, p. 14).

Diagnosis.—Sinistrally coiled turrilicone, with low apical angle (less than 20°) and roughly flat flank of the whorl; or-

namented by coarse tubercles in an upper row and more numerous finer tubercles in lower 2 or 3 approximated or coalesced rows, with a shallowly concave zone below the upper row; faint transverse riblets may extend upward and/or downward and scarcely cross the concave belt. Siphuncle runs along the upper shoulder or still higher immediately below or along the upper whorl seam, depending on the species.

Discussion.—The type species and its allied species *N. oberlini* (Dubourdieu, 1953) have been regarded as being well defined. The available specimens are, however, mostly fragmentary, without showing the details of the early growth stage or those of the last stage. The origin of this genus has been sought in *Ostlingoceras* (Klinger and Kennedy, 1978, p. 15).

In addition to the above two species from the lower Cenomanian, Cobban and Hook (1981) and Cobban *et al.* (1989) described five species from the middle and upper Cenomanian of New Mexico, of which one species, *N. viridenense* Cobban, Hook and Kennedy, occurs also in the upper Cenomanian of England (Wright and Kennedy, 1996). Furthermore, there are two new species (described below) in the middle Cenomanian of Hokkaido. Some of these species are represented by very small specimens, as shown by *N. procerum* Cobban, Hook and Kennedy, 1989 (p. 60, figs. 62, 95, O, P) and *N. asiaticum* sp. nov. (to be established below). They are, in their early growth stage, very similar to *Carthaginites kerimensis* (Pervinquière, 1907) (p. 101, pl. 4, figs. 18, 19) or *C. krorzaensis* Dubourdieu, 1953 (p. 66, pl. 4, figs. 49–52). Hence, the question might arise that *Neostlingoceras* is a junior synonym of *Carthaginites*. Until the characters of the later growth stages in *Carthaginites* can be made clear, *Neostlingoceras* should be used in accordance with the current definition.

Occurrence.—The genus has been recorded to occur in the Cenomanian of France, England, Germany, Poland, Romania, Turkmenistan, Kazakstan, Iran, Israel, Tunisia, Algeria, Madagascar, South Africa, New Mexico, Colorado, Wyoming, Texas and Japan. Although the type species and its allied species occur characteristically in the lower Cenomanian, other species are recorded from the middle and upper parts of the Cenomanian.

***Neostlingoceras carcitanense* (Matheron, 1842)**

Figure 3A–C, D–F

Turrillites carcitanensis Matheron, 1842, p. 261, pl. 41, fig. 4; Fabre, 1940, p. 242, pl. 5, fig. 7.

Turrillites morrisii Sharpe, 1857, p. 65 (*pars*), pl. 26, figs. 4, 6–7.

Hypoturrillites carcitanensis (Matheron). Kennedy, 1971, p. 59 (*pars*), pl. 6, figs. 1, 2, 4–6, 9, 10.

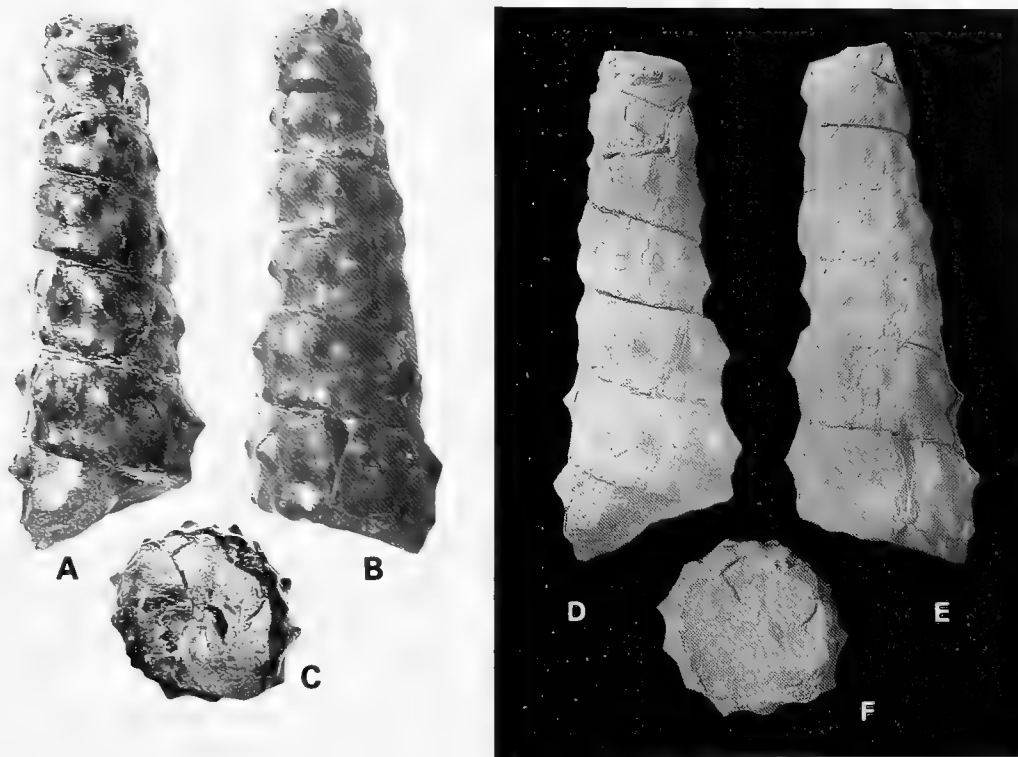


Figure 3. A–C, D–F. *Neostlingoceras carcitanense* (Matheron, 1842). Two lateral (A and B, 180° apart) and basal (C) views of GK. H8534, without whitening; similar views (D, E, F) of the same specimen with whitening. $\times 1$. Photos courtesy of M. Noda (A–C) and T. Nishida (D–F).

Turrilites (*Hypoturrilites*) *carcitanensis* (Matheron). Immel, 1979, p. 635, pl. 4, fig. 1.

Neostlingoceras carcitanense (Matheron). Klinger and Kennedy, 1978, p. 15 (*pars*), pl. 3, fig. G; Wright and Kennedy, 1996, p. 326, pl. 99, figs. 1–7, 9–15, 18, 19, 22; pl. 100, fig. 8; text-fig. 140B (with full synonymy).

Holotype.—By monotypy, the original of Matheron, 1842, pl. 41, fig. 4. We have not seen the specimen, which seems to be fragmentary as shown by Fabre's (1940, pl. 5, fig. 7) reillustration. The type locality is in southern France. Its present repository is uncertain (see Wright and Kennedy, 1996, p. 327).

Material.—GK. H8534 [= previous S. 40·8·15] (Figure 3A–C, D–F), collected by T. T. in 1965 at Loc. Ik1054 below the bridge called 'Katsura-Ohashi'. It was found in the dark green silty fine-grained sandstone of the Zone of *Mantelliceras japonicum*. Another crushed specimen, GK. H8556, was found by T. M. at Loc. R82 of the Soeushinai-Kontanbetsu area (for the location see Matsumoto and Okada, 1973, fig. 7). It was from the mudstone in the lower part of the Member My5. One of us (T. M.) examined the specimens from England (see above synonymy) at the Natural History Museum, London to compare them with ours.

Description.—Six continuous whorls are preserved in GK. H8534, which is 47 mm high altogether and 15.6 mm in diameter of the last whorl. The ratio of height to diameter in the exposed part of each whorl is roughly 5:9. The apical angle estimated from the preserved part of the shell is as low as 13°. The early part of the shell is lacking.

Each whorl is ornamented by an upper row of larger tubercles, 13 to a whorl, and a lower row of smaller, double tubercles 18 or 19 per whorl, above the lower whorl seam. The upper tubercle is pointed at the top and its base is bullate upward, whereas a concave spiral zone runs at about the

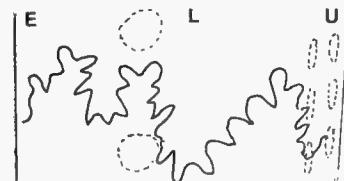


Figure 4. *Neostlingoceras carcitanense* (Matheron, 1842). External suture of GK. H8534 on the flank at $h = 7.8$ mm. Figure is about $\times 5.5$. Symbols as for Figure 2. Drawing by T. M.

midflank immediately below the row of major tubercles. The double tubercle of the lower row consists of a small subrounded upper one and rather clavate lower one which are closely set. Some of the upper ones are bullate upward, whereas the lower ones form the outer edge of the basal surface.

The suture is exposed on a part of the flank, showing L in the middle part of the flank, with saddles on either side of L. They are moderately incised at the middle growth stage (Figure 4).

Remarks.—When the genus *Neostlingoceras* was introduced, Klinger and Kennedy (1978, p. 15) considered that *N. carcitanense* (Matheron, 1842) is so variable that *N. oberlini* (Dubordieu, 1953) and some others were within its variation or might be subspecies in a successive sequence. Such an interpretation has been recently denied by Wright and Kennedy (1996, p. 327–328), with whom we agree.

Comparison.—The described specimen shows clearly the morphological characters of this species. It quite well resembles a specimen called SAS SM (Klinger and Kennedy, 1978, pl. 3, fig. G) from the Mzinene Formation, Cenomanian II, of the Skoenburg, Zululand.

Occurrence.—As for material. This species marks the basal zone of the Cenomanian in England, but it occurs in the beds of the next and still higher levels in Hokkaido.

***Neostlingoceras asiaticum* sp. nov.**

Figures 5 A–C, D–F, G–I; 6

Material.—Holotype is GK. H8536 [= previous S. 36·8·26] (Figure 5A, B, C) collected by T. T. in 1961 at Loc. Ik1103 from the middle part of the Cenomanian in the Mikasa area on the western wing of the Ikushunbetsu anticline. Two other specimens (paratypes) are GK. H8537 [= previous S.

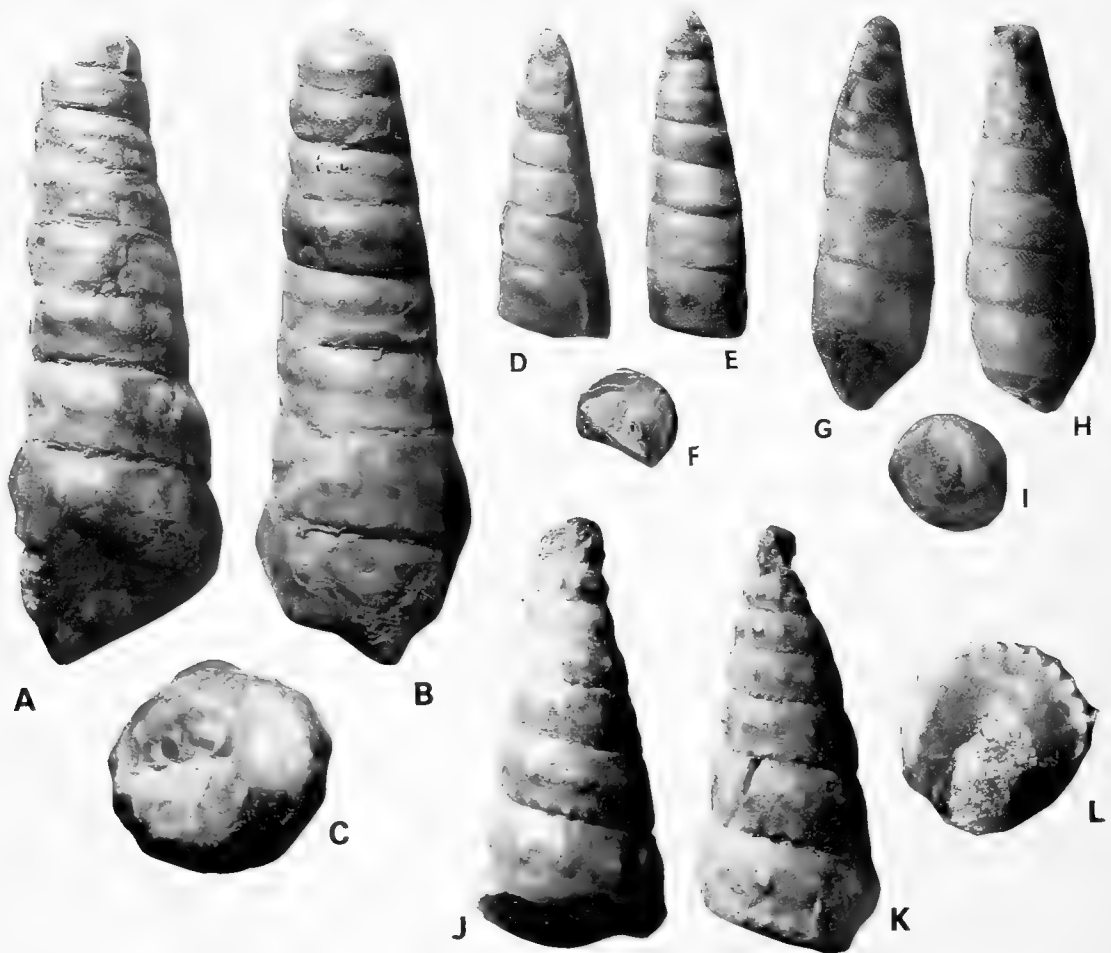


Figure 5. A–C, D–F, G–I. *Neostlingoceras asiaticum*, sp. nov. Two lateral (A and B, 180° apart) and basal (C) views of GK. H8536 (holotype). Similar views (D, E, F) of GK. H8537 and ditto (G, H, I) of GK. H8538. J–L. *Neostlingoceras cobbani* sp. nov. Two lateral (J and K, 180° apart) and basal (L) views of GK. H8535 (holotype). Figures are all $\times 3$. Photos courtesy of M. Noda.

Table 3. Measurements of *Neostlingoceras asiaticum* sp. nov.

| Specimen | NW | Hp | Ht | D | ap | h | d | h/d | T | t |
|-----------|-------|------|------|------|-----|-----|-----|------|----|----|
| GK. H8536 | 7.5 | 28.0 | 45.3 | 10.0 | 13° | 3.8 | 8.7 | 0.44 | 15 | 30 |
| GK. H8537 | 6 + a | 14.2 | 21.0 | 4.7 | 14° | 2.2 | 4.7 | 0.47 | — | — |
| GK. H8538 | 7 | 16.2 | 26.0 | 5.3 | 15° | 2.5 | 5.5 | 0.48 | 16 | 32 |

T = number of upper tubercles, t = number of lower tubercles, 6 + a = somewhat over 6. See Table 1 for other abbreviations.

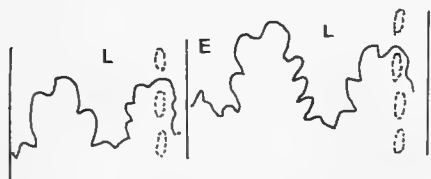


Figure 6. *Neostlingoceras asiaticum* sp. nov. External suture on the flank of two successive young whorls of GK. H8537 at h = 1.4 mm and 1.9 mm. Figure is about $\times 16$. Symbols as for Figure 2. Drawing by T. M.

55.3·10A] (Figure 5D, E, F) and GK. H3538 [= S. 55.3·10B] (Figure 5G, H, I) collected by T. T. in 1980 at the type locality (Ik1103). This locality belongs to the Abundance Zone of *Calycoceras* (*Newboldiceras*) *asiaticum*.

Diagnosis.—Shell slender with a low apical angle; whorl at early growth stage rather flat-sided, with rounded upper shoulder and shallow groove at midflank. Later, blunt nodes are developed on the upper shoulder and numerous minute tubercles are aligned along the lower edge of the flank. Suture fundamentally similar to that of *Ostlingoceras* (*O.*) *bechei*, but apparently simple on account of the small size of the shell (Figure 6).

Description.—The three specimens are all small as shown in Table 3. They preserve the shell layer for the most part. In GK.H3537, the smallest specimen, the suture is well shown at its preserved middle stage (2.3 mm in whorl height). It is rather simple, but the elements (L and the saddles on either side) exposed on the next whorl show more clearly minor indentations. L is situated on the concave zone of the midflank.

The holotype is the largest of the three specimens. Its earlier part is lacking. If its preserved last part be assumed to reach a part of the last whorl, the restored outline of the shell would be roughly 45 mm in height.

In every specimen the whorl junction is clearly impressed. The ratio of height to diameter in each whorl is low (less than 0.5). A gradual change of ornament with growth is evidently shown by the holotype. Two paratypes generally follow the holotype in this regard.

In young whorls a shallow and narrow, spiral groove runs at about the midflank and a low, spiral elevation above the groove forms a rounded shoulder in the upper part of the flank.

In the next step of growth, the upper elevation is faintly undulated and the lower edge of the whorl has numerous, tiny tubercles. Soon this is followed by broadening of the upper

elevation on which bluntly raised and upward bullate nodes are developed. The spiral groove below the upper elevation is somewhat shifted downward from the midflank and numerous small tubercles become distinct on the lower edge. The upper tubercles are 15 or 16 per whorl and the lower ones are twice as numerous as the upper ones. Both tubercles become gradually distinct with growth and a short riblet extends upward from each of the lower tubercles. Finally on the preserved last whorl narrow transverse ribs run obliquely downward (i. e., adorally) from some of the upper tubercles. Underneath the row of lower tubercles there is a train of narrowly clavate tubercles, which defines the margin of the basal surface of the whorl.

Comparison.—This species is unique among the nine species of *Neostlingoceras* in that its younger part is similar to *Carthaginites krorzaensis* Dubourdieu, 1953 (p. 66, pl. 4, figs. 49–52, text-fig. 20), from the upper Cenomanian of eastern Algeria, also to *C. cf. krorzaensis*, from the upper Cenomanian of England (Wright and Kennedy, 1996, p. 361, pl. 98, fig. 11), whereas its later whorls show the general characters of *Neostlingoceras*.

The present species somewhat resembles *N. bayardense* Cobban, Hook and Kennedy, 1989 (p. 60, figs. 95R, 96R), from the Zone of *Calycoceras canitaurinum* in New Mexico, but the latter has a still lower apical angle (11°), distinctly flatter flank and finer and more numerous tubercles in the upper row.

N. procerum Cobban, Hook and Kennedy, 1989 (p. 60, figs. 62, 95 O–Q, S), from the upper Cenomanian *Metoicoceras mosbyense* Zone in New Mexico, is also similar to the younger part of the present species. Its shell is, however, more slender with a lower apical angle (10°). In later growth stages the nodes in the upper row are more distinct and coarser in *N. asiaticum*. It should be noted that transverse ribs occur at the late growth stage in both species.

Occurrence.—As for material. It should be noted that the present species is fairly close in geological age to *N. bayardense* mentioned above.

Neostlingoceras cobbani sp. nov.

Figure 5J–L

Material.—Holotype, designated herein, is GK. H8535 [= previous S.36.3·28] (Figure 5J, K, L), collected by T. T. in 1961 at loc. Ik1103 of Nishikatsurazawa, from the middle Cenomanian part of the Mikasa Formation on the western wing of the Ikushunbetsu anticline. At present it is the sole available material for this rare but noteworthy species.

Specific name.—In honor of William A. Cobban, who has

Table 4. Measurements of *Neostlingoceras cobbani* sp. nov.

| Specimen | NW | Hp | Ht | D | ap | h | d | h/d | T | t |
|-----------|-------|------|------|-----|-----|-----|-----|------|----|----|
| GK. H8535 | 6 + a | 20.0 | 25.5 | 8.8 | 20° | 3.5 | 7.5 | 0.47 | 10 | 25 |

Abbreviations as for Table 3.

made a remarkable contribution to palaeontology and biostratigraphy.

Diagnosis.—A species of *Neostlingoceras* that shows a comparatively less acute apical angle for the genus, distantly disposed and rather bluntly elevated tubercles of the upper row, shallower concave zone at midflank and numerous, small tubercles of the lower row. Small size of the shell appears to be diagnostic, but is not necessarily definite.

Description.—This specimen preserves six whorls, but its very apex and late whorls are unpreserved. It is small, as shown in Table 4, although the true size of the completely preserved original shell is not known. The proportion of height to diameter of each whorl is less than 0.5. The apical angle as estimated from the preserved part of the shell is 20°.

The upper part of the outer exposed whorl face slopes down to the upper row of tubercles where a shoulder is formed. The tubercles of this row are distant and not numerous; 10 per whorl on average. Each of them is a bluntly pointed node which is broadened but lowered upward. A shallowly concave spiral zone runs below the upper row of major tubercles. Minor tubercles of the lower row are numerous, 25 per whorl. They are arranged in a single row immediately above the lower whorl seam, but each of them seems to be double, as it is granular in lateral view but is rather clavate in lower view, forming the outer edge of the lower face of the whorl. In other words the lower tubercles may be those of united 2nd and 3rd rows. Sometimes faint riblets may extend upward from the lower tubercles across the concave zone below the row of major tubercles. On the lower face of the whorl ribs are scarcely discernible.

The suture is not well traced. The preserved last whorl is still septate, showing minor indentation on the lobes of L, U and adjacent saddles.

Comparison.—Although the specimen is small, it shows the generic characters of *Neostlingoceras*. It is distinguished from *N. carcitanense* by the diagnosis (see above). Although the ratio of height to diameter of each whorl may vary to some extent within a species, it is generally smaller in the present species than in the cases of *N. carcitanense*, *N. oberlini* and also *N. kottlowskii* Cobban and Hook, 1981 (p. 26, pl. 4, figs. 1–28; Cobban, 1984, p. 17, pl. 4, fig. 9; Cobban *et al.*, 1989, p. 60, fig. 95 A–F). *N. kottlowskii* is closer in geological age to the present species than the other two.

Occurrence and distribution.—As for material; unique at present.

Genus *Hypostlingoceras* nov.

Type species.—*Hypostlingoceras japonicum* sp. nov. (described below).



Figure 7. A, B. *Hypostlingoceras japonicum* gen. et. sp. nov. Lateral (A) and basal (B) views of GK.H8542 (holotype). Figures are x2. Photos courtesy of M. Noda.

Diagnosis.—Turrilitid ammonoids which show peculiar change of characters with growth. Whorls in early growth stages have coarse or strong tubercles at about the midflank and numerous, minute tubercles in at least two lower rows. Sooner or later the tubercles at midflank gradually weaken and become sparse, whereas transverse ribs intervene between the tubercles. Finally the midflank tubercles disappear, while numerous transverse ribs predominate, and thus the ornamentation as well as the whorl shape becomes quite similar to that of *Ostlingoceras*.

Discussion.—On account of its more or less slender shell shape and small size, this genus resembles *Neostlingoceras* rather than *Hypoturrilites* in its youth. In more or less later growth stages it is quite similar to *Ostlingoceras*. The stage at which the characters of the *Neostlingoceras* type change to those of the *Ostlingoceras* type varies to some extent, and the change occurs more or less gradually. Based on the above facts, we presume that *Hypostlingoceras* may have been derived from *Ostlingoceras* in parallel with *Neostlingoceras*. The type specimens are never artificial chimeras.

Occurrence.—At present this genus is represented by two species from the lower Cenomanian in the Mikasa area of Hokkaido. More material should be searched for to determine clearly the geological and geographical distribution as well as the phylogenetic relationships of this genus.

***Hypostlingoceras japonicum* sp. nov.**

Figures 7A, B; 8A–E; 9A–E; 10

Material.—Holotype, designated herein, is GK. H8542 [= previous S. 36·7·25] (Figures 7A, B; 8A, B, C, D, E), collected by T. T. in 1961 from the lower part of the Mikasa Formation exposed on the Ganseki-zawa, i. e., the eighth branch of the Kami-ichino-sawa, a tributary of the River Ikushunbetsu. Paratype is GK. H8541 [= previous S. 39·9·11] (Figure 9A, B, C, D, E) collected by T. T. in 1964 at Loc. 7045 of T. T. in the Suido-no-sawa, a short branch of the River Ikushunbetsu. The beds at the above two localities are referred to the *Mantelliceras japonicum* Zone, and are early Cenomanian in age.

Diagnosis.—Shell shape is slender, with low apical angle, and rather small. Whorls in youth subtrapezoid in lateral view, with square shoulder at midflank where coarse and strong tubercles are disposed at intervals. Then comes a transitional stage, where whorl is subrounded, midflank tubercles weaken and extend upward to ribs and additional intervening ribs occur. Whorls in later growth stages gently inflated on side and ornamented densely by numerous transverse ribs. Minute tubercles are aligned on the lower two narrow ridges throughout growth.

Description.—The two specimens, GK. H8542 and GK. H8541, are much different in size but similar in their slender

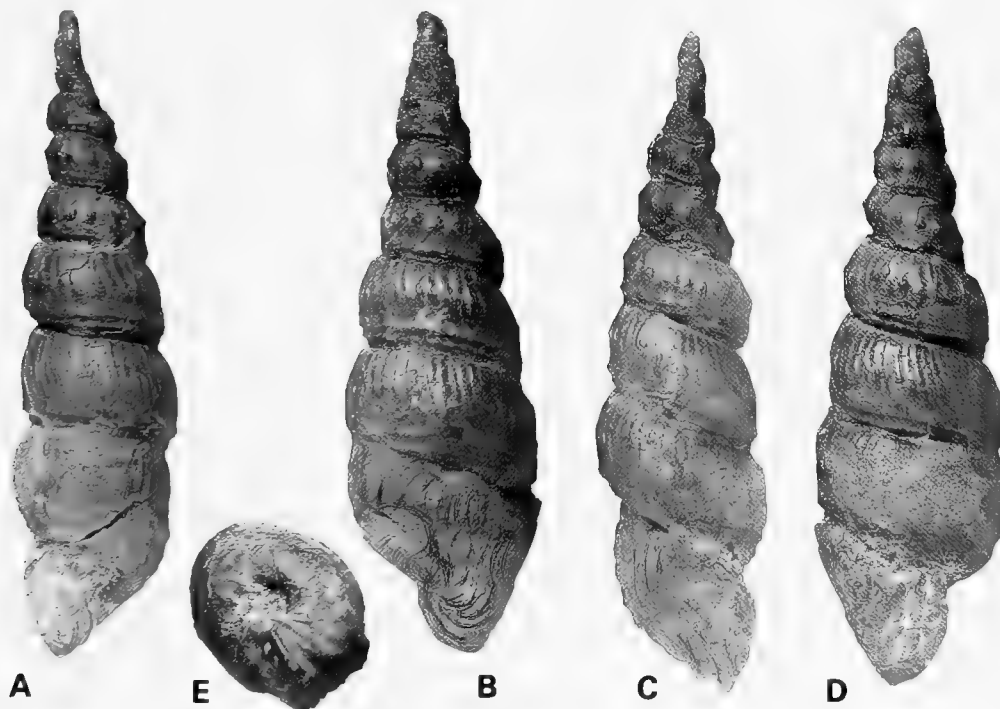


Figure 8. A–E. *Hypostlingoceras japonicum* gen et sp. nov. Four lateral (A, B, C, D, successively 90° apart clockwise) and basal (E) views of GK.H8542 (holotype). Figures are $\times 1.2$. Photos courtesy of T. Nishida.

Table 5. Measurements of *Hypostlingoceras japonicum* sp. nov.

| Specimen | NW | Hp | Ht | D | ap | h | d | h/d | R | T | t |
|-----------|-------|------|------|-----|-----|------|------|------|----|----|----|
| GK. H8542 | 8 + a | 69.0 | 80.0 | 20 | 18° | 11.0 | 19.0 | 0.58 | 40 | 16 | 30 |
| GK. H8541 | 7 + a | 26.5 | 34.0 | 8.5 | 18° | 4.2 | 7.4 | 0.57 | 32 | 15 | — |

Abbreviations as for Tables 1 and 4. T and t are measured on the whorl at 2 volutions earlier than that where h, d, and R are measured.

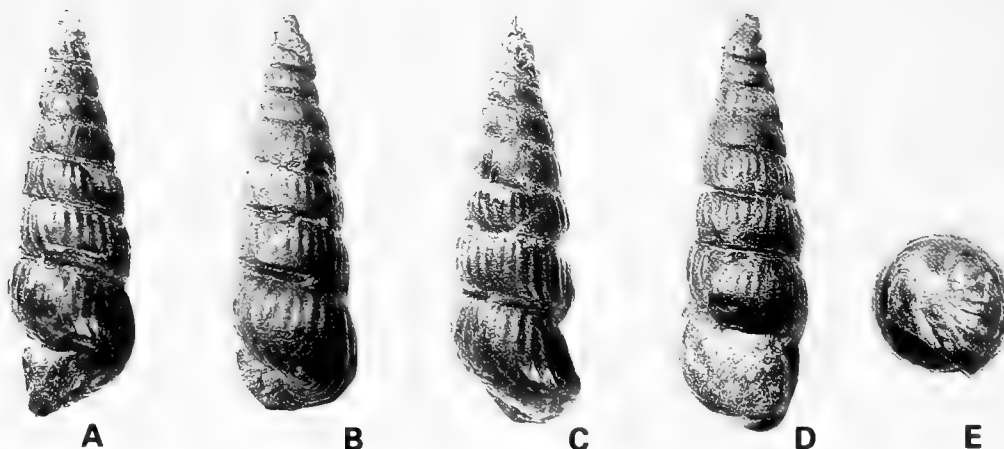


Figure 9. A–E. *Hypostlingoceras japonicum* gen. et sp. nov. Four lateral (A, B, C, D, successively 90° apart clockwise) and basal (E) views of GK.H8541 (paratype). Figures are $\times 2$. Photos courtesy of M. Noda.

shell shape with a low apical angle (about 18°) and the proportion of the flank height and diameter of each whorl is slightly above 0.5 (see Figures 7–9 and Table 5). The stage characterized by strong midlateral tubercles is manifested by several young whorls in the two specimens, although the youngest part is destroyed or unpreserved. The change in the whorl shape and ornamentation is evident in both specimens, but it occurs in the whorl at a diameter of about 15 mm in GK. H8542, whereas it occurs at a diameter of about 5 mm in GK. H8541. An *Ostlingoceras*-like late stage continues for fully 3 whorls in the smaller specimen (GK. H8541) and for 2.5 whorls in the larger one (GK. H8542).

In the larger specimen the longitudinal ribs become denser and more numerous on the whorl of the later growth stage (Figure 8). However, near the preserved last part a few ribs strengthen and markedly curve on the convex basal surface (Figure 7B). However, as the last whorl is partly destroyed, we cannot confirm the real peristome. In the smaller specimen the ribs do not become particularly dense and numerous in the preserved last whorl. They curve rather moderately on the convex lower surface (Figure 9).

Almost throughout growth, in both specimens, small tubercles are aligned in two rows on the narrowly raised ridges which are separated by a narrow groove. At first these minor tubercles correspond in number and disposition to the major ones, but soon they become more numerous and clavate. These two rows of minor tubercles correspond to

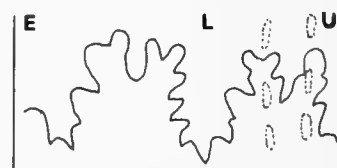


Figure 10. *Hypostlingoceras japonicum* gen. et sp. nov. External suture of GK. H8541 (paratype) on the preserved last whorl at $h = 5$ mm and $d = 8.2$ mm. Figure is about $\times 9$. Symbols as for Figure 2. Drawing by T. M.

the second and third rows in certain species of *Ostlingoceras* (*Ostlingoceras*). The second row forms the lower edge of the flank and the third row runs along the lower whorl seam.

In the early stages there is a concave spiral zone below the subangular zone of strong tubercles. In the transitional and later stages, the concave zone shifts downward and the ribs have more or less weakened smaller tubercles above this zone. These minor tubercles may be so reduced that they may be sometimes expressed as faint swellings. The ribs extend further to run across the concave zone with gentle sinuosity and weakening and are connected with minor tubercles of the second row. In addition to the tubercles of

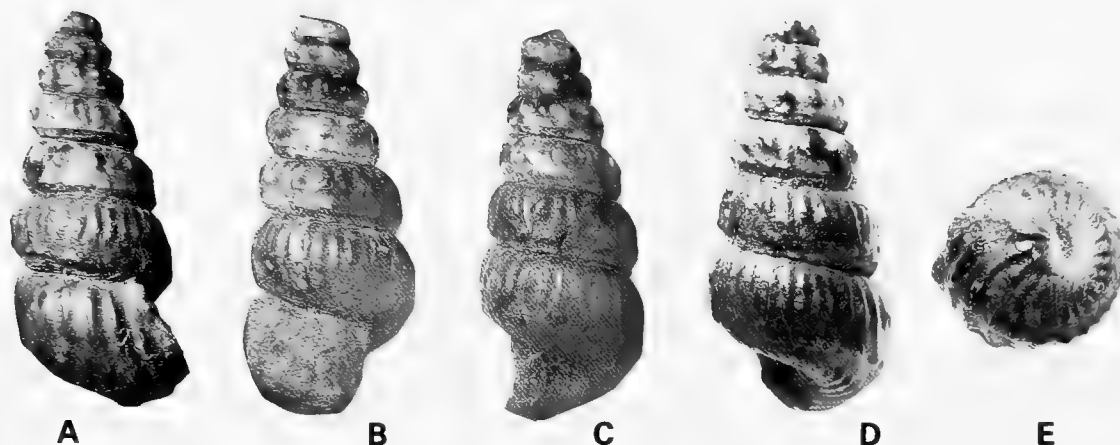


Figure 11. A–E. *Hypostlingoceras mikasaense* gen. et sp. nov. Four lateral (A, B, C, D, successively 90° apart clockwise) and basal (E) views of GK.H8540 (holotype). All figures are $\times 2.1$. Photos courtesy of T. Nishida (A–C) and M. Noda (D, E).

Table 6. Measurements of *Hypostlingoceras mikasaense* sp. nov.

| Specimen | NW | Hp | Ht | D | ap | h | d | h/d | R | T | t |
|-----------|----|------|------|------|-----|-----|------|------|----|----|----|
| GK. H8540 | 6 | 26.0 | 32.0 | 13.0 | 30° | 4.6 | 10.3 | 0.45 | 30 | 14 | 23 |

Abbreviations as for Table 5.

the third row, those of the fourth row may be discernible on some ribs of the basal surface.

A septal suture is observed on the preserved last whorl of the smaller specimen (see Figure 10).

Discussion.—The specimen, OM.II-497, illustrated as '*Turrilites* cf. *costatus* Lamarck' by Ikegami and Omori (1957, pl. 14, fig. 3), from their Unit MK1 (= Member IIb of Matsumoto, 1965, fig. 4; 1991, p. 22–24), was listed under *Ostlingoceras* (*O.*) aff. *colcanapi* (Boule, Lemoine and Thévenin, 1907) by Wright and Kennedy (1996, p. 323). Its figure shows, however, a more slender shell shape with a lower apical angle and its younger whorls have a row of coarse tubercles at about midflank. It is probably another example of this species. Regrettably, the original specimen is missing at present.

Occurrence.—As for material.

Hypostlingoceras mikasaense sp. nov.

Figure 11A–E

Material.—Holotype is GK. H8540 [= previous S. 51·7·4] (Figure 11A, B, C, D, E), collected by T. T. in 1976 at a locality on the northeastern rivulet ['Migimata'] of the Ganseki-zawa, i. e., the eighth branch of the Kami-ichi-no-sawa, a tributary of the River Ikushunbetsu. The exposed rock of the type locality is referred to the *Mantelliceras japonicum* Zone of the Mikasa Formation.

Diagnosis.—Shell small, with a moderate apical angle, about 30° as estimated from the preserved part. Whorls in

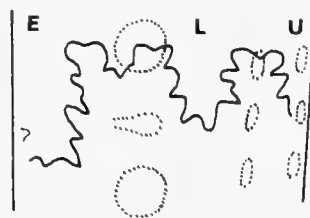


Figure 12. *Hypostlingoceras mikasaense* gen et sp. nov. External suture of a young stage at $h = 4.2$ mm. Figure si about $\times 9.5$. Symbols as for Figure 2. Drawing by T. M.

youth subtrapezoid in lateral view with shoulder at about the midflank, where coarse and strong tubercles are aligned. Change of ornament at transitional growth stage generally follows that of the type species. Later whorls show moderately to gently convex flanks and ornamentation like that of *Ostlingoceras* (*O.*) *bechei* (Sharpe, 1857).

Description.—The holotype consists of about 6 whorls, but its apical part is lacking. The preserved part of the shell is 26 mm high and its diameter at the last whorl is 13 mm. The apical angle estimated from the preserved part of the shell is about 30°. Whorls are tightly in contact, with a fairly deeply impressed junction. The ratio between flank height and diameter in each whorl is about 0.45 (see Table 6).

The shape of a young whorl in lateral view is trapezoid, with an angular shoulder at about the midflank, where strong tubercles are aligned at moderate intervals, numbering 12 per whorl. Another row of smaller tubercles runs on a narrow ridge slightly above the lower whorl seam. On the preserved first whorl these lower tubercles are fairly coarse and correspond in number and disposition to the upper tubercles. Soon the upper strong tubercles are bullate and the lower tubercles become finer and tend to be clavate.

In the transitional stages the upper tubercles are weakened, transversally elongated and distantly arranged, whereas a few nodeless ribs occur in the intervening space. The minor tubercles on the lower spiral ridge are disposed approximately on the extension of the elongated tubercles and intervening ribs. Throughout the above-described stages there is another row of clavate tubercles along the lower whorl seam. There is a narrow but distinct spiral groove between the two lower rows of minor tubercles.

In the late stages, including the late transitional substage, the whorl develops a more rounded shape, showing a gently convex flank. It is ornamented by numerous transverse ribs, numbering 32 in the preserved last whorl. Above the second row of minor tubercles there is a shallowly concave spiral zone. The ribs run across this concave zone with slight weakening and sinuosity. In the preserved last whorl the third row of minor tubercles is not clavate but elevated at the markedly curved point of the ribs on the marginal part of the basal surface. Some of the tubercles seem to be doubled, suggesting incorporation of the remnants of the tubercles of the fourth row (Figure 11E). The ribs extend further toward the narrow umbilicus with a gentle curvature.

The septal suture is partly exposed on the flank of a rather young whorl, showing half of E, the E-L saddle, entire L and a part of the L-U saddle. L is situated on the concave zone below the upper row of the tubercles. These elements are indented (Figure 12).

Comparison.—With respect to the general change of characters with growth, this species is assigned to the genus *Hypostlingoceras*. It is distinguished from *H. japonicum* in having a larger apical angle, smaller ratio of h/d in each whorl, stronger midflank tubercles in youth and somewhat coarser and less numerous ribs on the later whorls.

The whorls of this species in late growth stages are fairly similar to *Ostlingoceras* (*Ostlingoceras*) *bechei* (Sharpe) in shell shape and ornamentation, although this does not necessarily imply a direct phylogenetic relationship.

Occurrence and distribution.—As for material. At present this species is known solitarily in the lower part of the Cenomanian of Hokkaido.

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Late Paleocene to early Eocene planktic foraminiferal biostratigraphy of the Dungan Formation, Sulaiman Range, central Pakistan

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Abstract. The Paleogene marine sequences of the Dungan, Shaheed Ghat, Baska and Kirthar Formations are exposed at several places in the Sulaiman fold and thrust belt in central Pakistan. The lowermost Dungan Formation unconformably overlies the open marine Maastrichtian Pab Sandstone, being distributed widely along both limbs of the Zinda Pir Anticline area and in the Rakhi Nala area. The Dungan Formation is composed mainly of black-colored siltstone with some intercalations of sandstone in the base and many interbeds of limestone in the upper part. The strata from all three sections have yielded abundant and well-preserved Paleocene-Eocene planktic foraminifers and about 50 species belonging to nine genera are identified from this sequence. Zones P3 to P7 of the tropical zonal schemes were recognized, furthermore, Zones P3 and P4 are subdivided into two subzones (Subzones A and B), respectively. These assemblages contain a new species *Globanomalina rakhiensis* in the Rakhi Nala section. A late Paleocene through early Eocene age is assigned to the Dungan Formation. The quantitative data of each species indicates that the Dungan Formation was deposited in a relatively deep to open marine environment, probably forming a continental slope dipping from east to west.

Key words: Biostratigraphy, Dungan Formation, Pakistan, Paleocene-Eocene, paleoenvironment, planktic foraminifera, Sulaiman Range

Introduction

A Mesozoic to Paleogene sedimentary sequence is widely exposed along the northwestern margin of the Indian Subcontinent in central Pakistan. These strata were deposited during the closing of the Tethys Ocean and form several fold-and-thrust belts of over 100 km width along a series of lobes in the Kirthar, Sulaiman, and Salt Ranges from south to north (Cheema *et al.*, 1977; Humayon *et al.*, 1991; Warwick *et al.*, 1998). The Paleogene sequence of the Sulaiman Range which overlies the Mesozoic marine shelf sediments consists of the Paleocene to Eocene Dungan Formation, the early Eocene Shaheed Ghat and Baska Formations, and the middle to late Eocene Kirthar Formation. Latif (1961) and Samanta (1973) reported many Paleocene-Eocene planktic foraminifers and their zonation from the Rakhi Nala section located in the eastern Sulaiman Range (Figure 1). Jones (1997) also showed the age of the Dungan Formation using the planktic foraminifers recovered

from three samples from the northern part of the Sulaiman Range. Warraich and Natori (1997) also established the Paleocene-Eocene planktic foraminiferal biostratigraphy on the western side of the Zinda Pir Anticline region, and recognized the following nine zones: the *Morozovella angulata*, *Globanomalina pseudomenardii*, *Morozovella velascoensis*, *M. subbotinae*, *M. formosa formosa*, *M. aragonensis*, *M. spinulosa/Truncorotaloides topilensis*, *Catapsydrax howei* and *Globigerina officinalis* zones. However, this biostratigraphic work is still preliminary and further detailed work is needed for correlation with the recently revised standard zonal schemes of Berggren *et al.* (1995) and Olsson *et al.* (1999).

The main objectives of this paper are to establish a complete biostratigraphic zonation of the Dungan Formation distributed in the Zinda Pir Anticline and the Rakhi Nala regions of the Sulaiman Range, and to correlate zones established in these regions with standard zones of the tropical-subtropical latitudes, and with those recognized in the other

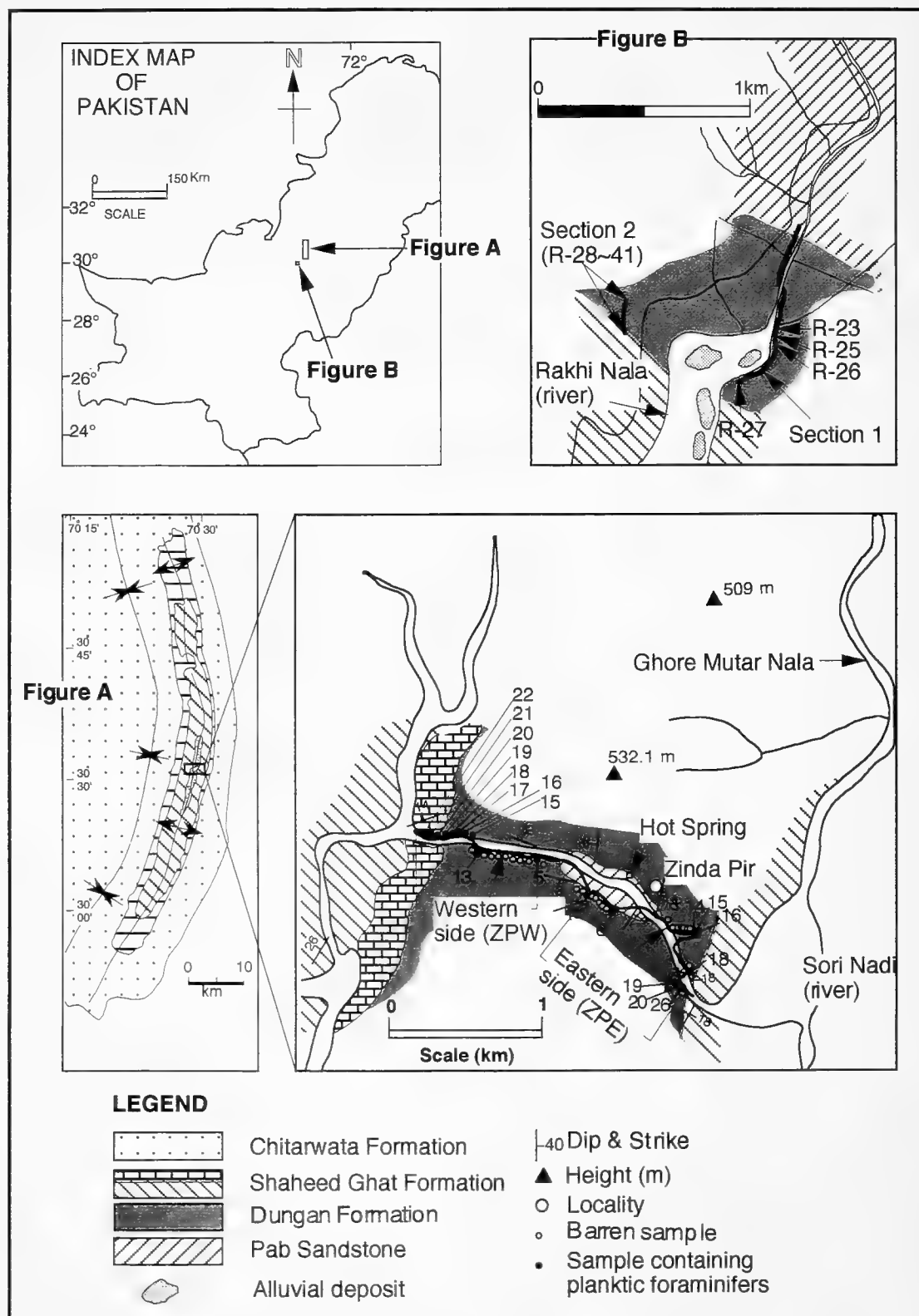


Figure 1. Route maps of the Rakhi Nala and the Zinda Pir sections of the eastern Sulaiman Range, central Pakistan.

regions of the Indus Basin. We also discuss the faunal changes and depositional environment of the Dungan Formation using quantitative foraminiferal data.

Materials and methods

We carried out systematic sampling along both sides of the Zinda Pir Anticline and in the Rakhi Nala section covering the entire sequence of the Dungan Formation (Figure 1). Some 54 samples (22 samples coded ZPW and 32 samples coded ZPE) were obtained along the western and the eastern limbs of the Zinda Pir Anticline, and 41 samples (coded R) were collected from the Rakhi Nala section. These samples were collected at 1- to 5-meter intervals. Because siltstone samples were very hard, all samples (each weighing 100g) were first treated with sodium sulfate (Na_2SO_4), and later with tetraphenylborate (NaTPB). The disaggregated samples were washed using a 63 μm sieve.

Population counts for planktic foraminifers are based on random splits of 200 to 300 specimens. To remove juvenile forms, specimens over 150 μm were picked and identified; however, the smaller fractions were also scanned for recognition of small-sized species. The faunal reference list is given in Appendix 1.

Lithostratigraphy

The Paleogene sequences exposed in the Zinda Pir and Rakhi Nala sections of the investigated areas consist of the Dungan and the Shaheed Ghat Formations in ascending order (Figure 1). The Dungan Formation forms the basal part of the Paleogene sequence, unconformably overlying the Maastrichtian Pab Sandstone (Kazmi, 1995, Nomura and Brohi, 1995, this study). Eames (1952) was the first who described the lithostratigraphy of the lower Paleogene strata of both the Zinda Pir and Rakhi Nala areas in detail. He divided this sequence into four lithological units in both areas (Figure 2). Cheema *et al.* (1977) and Kazmi (1995) summarized his several units and gave the name of the Dungan Formation to the mudstone-dominated sequences. For example, Kazmi (1995) included many lithological units

defined by many previous workers into the Dungan Formation (Figure 2).

We divided the strata distributed in the studied area into three formations according to the lithology of Kazmi (1995). The lowermost strata of the Maastrichtian Pab Sandstone consist of white, cream-to brown-colored, thick- to massive-bedded, medium to coarse-grained quartzose sandstone with intercalations of shale and argillaceous limestone in the study areas. The Dungan Formation overlying the Pab Sandstone represents dark-black colored siltstones interbedded with hard quartzitic-glaucinitic sandstone beds in the lower part and thin-to thick-bedded, dark-gray limestone weathering brown-buff in the upper part. The interbeds of sandstone are abundant in the Rakhi Nala, while those of limestone are common in the Zinda Pir.

It is noteworthy that the thickness of the Rakhi Nala section (312 m) is twice that of the Zinda Pir sections (135 m). In the Sulaiman Range, while contact of the Dungan Formation with the overlying Shaheed Ghat Formation is described as conformable (Cheema *et al.*, 1977; Shah, 1990, Kazmi, 1995). However, we describe this contact as unconformable based on the presence of the conglomeratic to brecciated limestone bed in the lowermost part of the Shaheed Ghat Formation (Figures 3–6). Previous workers (Eames, 1952; Cheema *et al.*, 1977; Shah, 1990, Kazmi, 1995) did not report this conglomeratic to brecciated limestone bed. Moreover, this result is also supported by the nonexistence of Zone P6 (Figures 3–6). Thickness of the conglomeratic to brecciated limestone bed is 16 m in the Zinda Pir sections that pinches out at Rakhi Nala. However, in the Rakhi Nala section, there is another conglomeratic to brecciated bed (1 m) which is stratigraphically younger than those of the Zinda Pir sections (Figure 6). This limestone contains shallow marine fossils such as larger foraminifers and bivalves (*Vasticardium* and *Chlamys* species) embedded in a calcareous matrix containing a pelagic fauna.

Biostratigraphy

Among 32 and 22 samples collected from the Dungan

| Eames (1952) | | Cheema et al. (1977) | Kazmi (1995) | This work |
|------------------------|----------------------------|-------------------------|---------------------------|---------------------------|
| Rakhi Nala | Zinda Pir | | | |
| Upper Rakhi Gaj Shales | Ghazij Shales | Ghazij Fm. | Shaheed Ghat Formation | Shaheed Ghat Formation |
| | Zinda Pir Ls. (upper part) | | | |
| Lower Rakhi Gaj Shales | Zinda Pir Ls. (lower part) | Dungan Fm. | Dungan Formation | Dungan Formation |
| | Zinda Pir Shales | | | |
| Gorge Beds | Quartzose Sandstone | Bara Fm. | | |
| Venericardia Shales | | Khadro Fm. | | |
| Pab Sandstone | | Pab Sandstone | Pab Sandstone | Pab Sandstone |

Figure 2. Lithostratigraphic subdivisions and correlation of the early Tertiary strata exposed in the Sulaiman Range proposed by different workers.

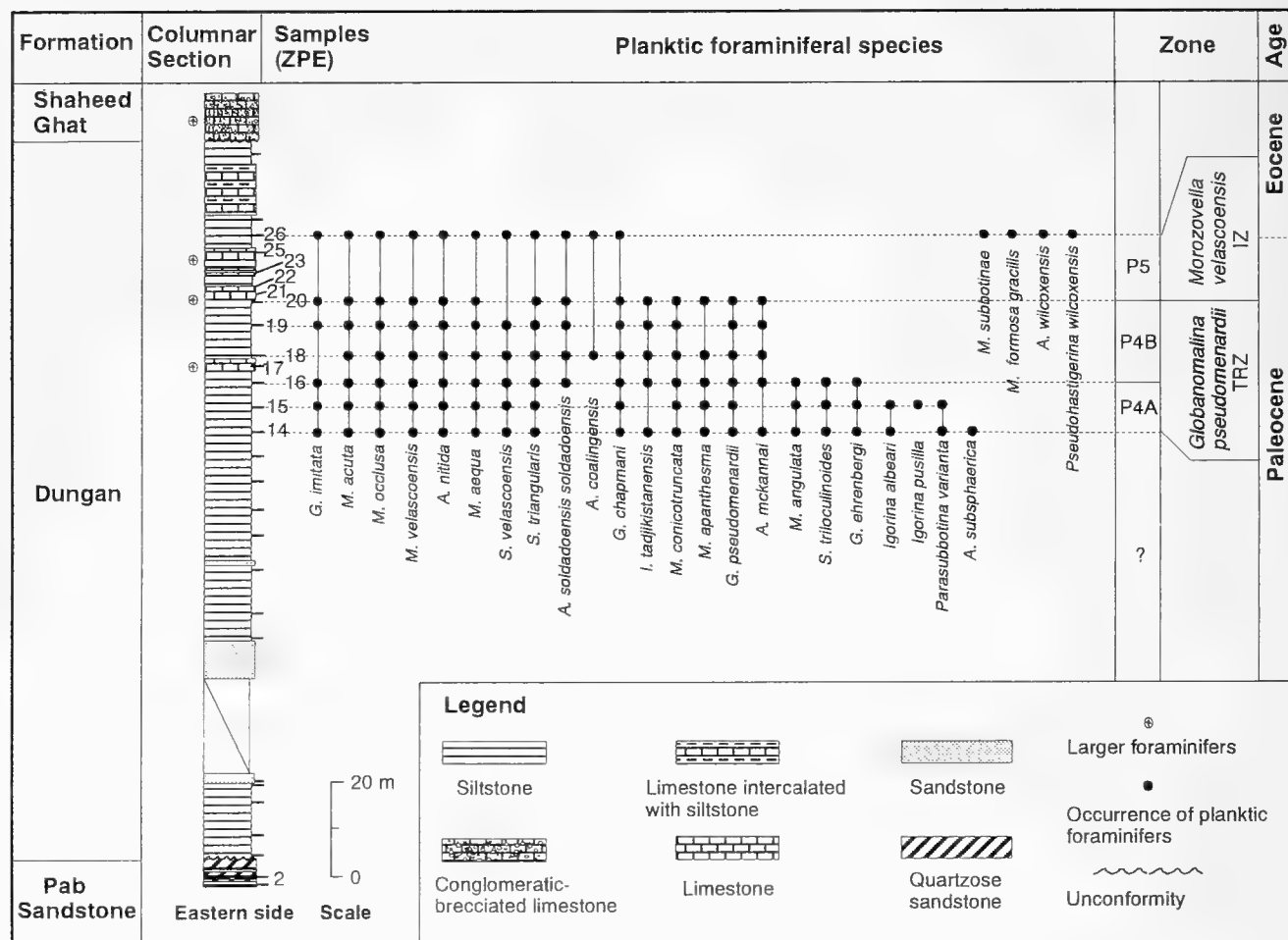


Figure 3. Measured columnar section along the eastern limb of the Zinda Pir Anticline showing lithostratigraphic sequences, sample locations, and biostratigraphic distribution of the recovered planktic foraminifers. The numbers indicate the samples containing planktic foraminifers.

Formation along the eastern and western limbs of the Zinda Pir Anticline, 7 and 11 samples yielded planktic and benthic foraminifers, respectively. The individual specimens of the planktic foraminifers recovered from the western side of the Zinda Pir Anticline are abundant and better preserved than those from the eastern side. Some 30 species belonging to 7 different genera of planktic foraminifers were identified in the Zinda Pir sections (Appendix 3).

In the Rakhi Nala section, 16 samples out of 41 yielded abundant and well-preserved foraminifers. The planktic foraminiferal assemblage recovered from this section comprised 51 species belonging to 10 genera (Appendix 3).

Two standard Paleogene zonal schemes have been established in the low-latitude regions. One is represented by Bolli's zonation and its revisions (Bolli, 1957, 1966; Toumarkine and Luterbacher, 1985). The other one is the P-zonation of Blow (1979) and its modifications (Berggren and Miller, 1988; Berggren *et al.*, 1995). Recently, Berggren and Norris (1997) and Olsson *et al.* (1999) have

published updated versions of the Paleocene P-zonal system and the phylogeny.

The Paleogene fauna recovered from the Dungan Formation included abundant tropical and subtropical indicators, suggesting a habitat of tropical-subtropical Tethyan waters. Hence, the Paleogene international zonal schemes proposed by Berggren *et al.* (1995) and Olsson *et al.* (1999) are basically applicable to the faunal assemblage of the Dungan Formation (Figure 7). This formation is divided into five biostratigraphic intervals that correspond to Zones P3 to P7 of Berggren's zonation (Figure 7). However, we have subdivided Zone P4 of Berggren and Norris (1997) and Olsson *et al.* (1999) into two subzones instead of three as an extension of the stratigraphic range of *A. subsphaerica* is recorded in this region. Moreover, we have used some different datum levels as boundaries of subzones due to sporadic occurrence of index species in the lower portions of all three sections.

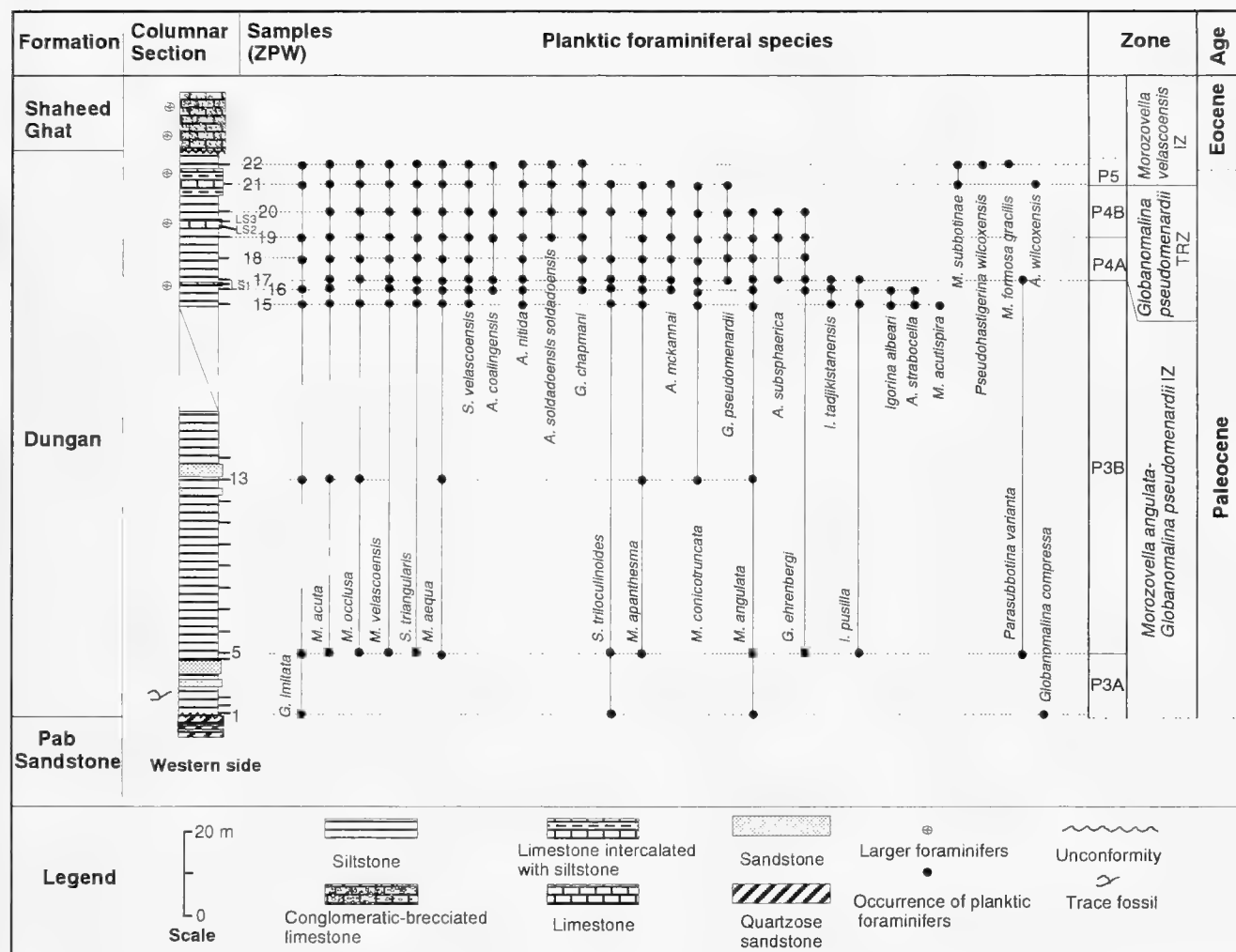


Figure 4. Measured columnar section along the western limb of the Zinda Pir Anticline showing lithostratigraphic sequences, sample locations and biostratigraphic distribution of the recovered planktic foraminifers. The numbers indicate the samples containing planktic foraminifers.

Paleocene Zones of the Dungan Formation

P3. *Morozovella angulata*/*Globanomalina pseudomenardii* Interval Zone

Zone P3 of Berggren and Norris (1997) and Olsson *et al.* (1999) is defined as the interval zone between the first appearance datum (FAD) of *Morozovella angulata* and the FAD of *Globanomalina pseudomenardii*. They also have subdivided Zone P3 into Subzones P3a and P3b using the FAD of *Igorina albeari*. In this paper, however, we cannot use their subzones because of the sporadic occurrence of *I. albeari* (Figures 3–5). Instead, we defined two regional subzones as described below, using the FAD of *M. acuta*.

P3A. *Morozovella angulata* -*M. acuta* Interval Subzone

Definition.—The lower boundary of this zone is not defined because of the missing sequence in the Zinda Pir and nonoccurrence of any planktic foraminifers in the Rakhi

Nala. The upper boundary is placed at the FAD of *Morozovella acuta* (Figure 4).

Occurrence.—This subzone is found restrictedly in the western section of the Zinda Pir Anticline (Figures 1, 4). Planktic foraminifers in this zone are not abundant, with the total number of specimens per sample ranging from 20 to 76 per sample. The rare occurrence of *M. angulata* is observed in Sample ZPW-1, associated with *Globanomalina imitata*, *G. compressa*, and *Subbotina triloculinoides*.

Correlation and age.—The FAD of *M. acuta* is a reliable datum in the tropical regions, being placed within Subzone P3b of Berggren and Norris (1997) and within the *Planorotalites pusilla pusilla* Zone of Toumarkine and Luterbacher (1985). The other index species of the Dungan Formation is *G. compressa*, which disappears within Zone P3a of Berggren and Norris (1997). The absence of *M. acuta* and cooccurrence of *M. angulata* and *G. compressa*

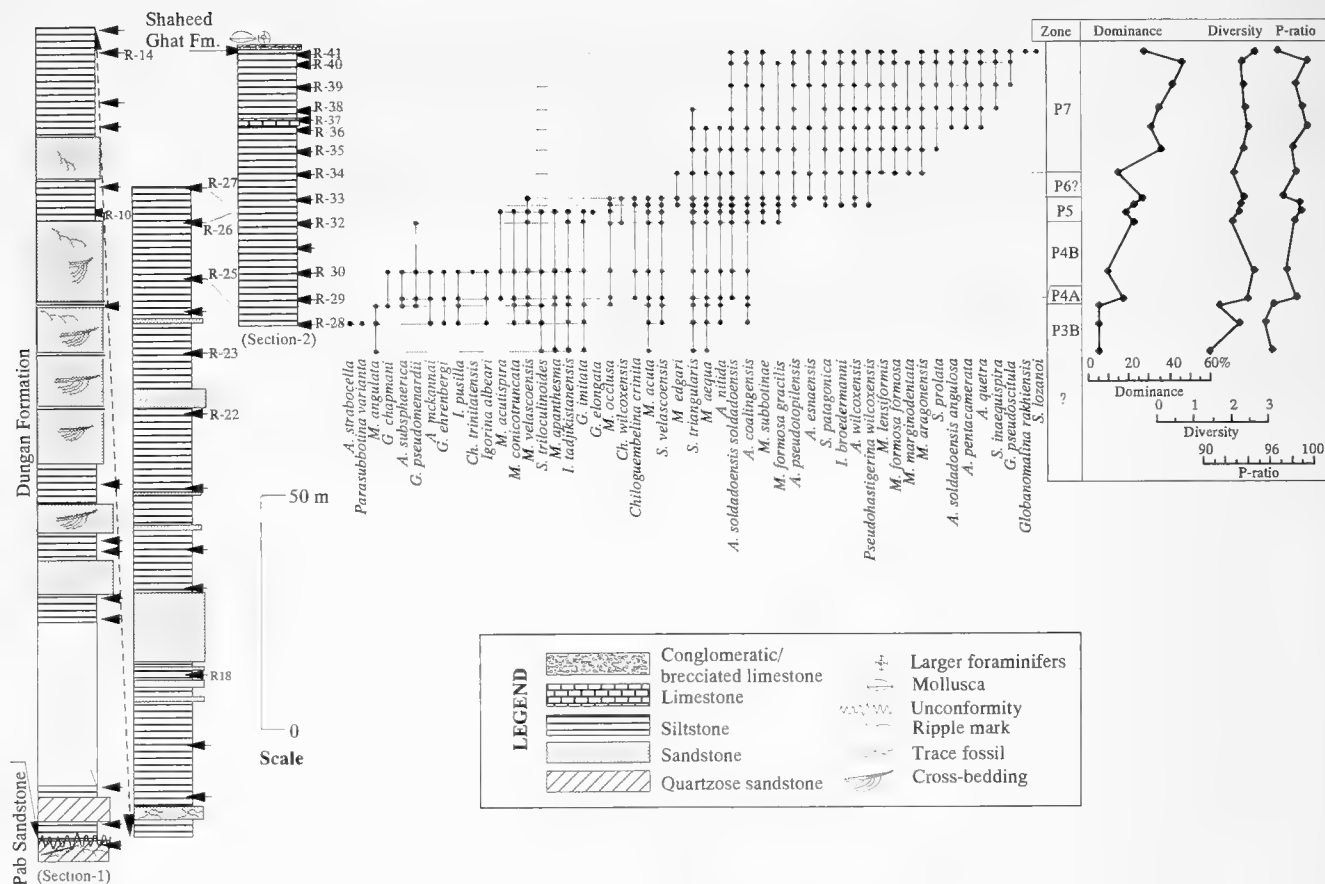


Figure 5. Measured columnar section along the Rakhi Nala (river) showing lithostratigraphic sequences, sample locations and biostratigraphic distribution of the recovered planktic foraminifers. The numbers indicate the samples containing planktic foraminifers. In addition, the results of quantitative analysis consisting of dominance (the most abundant species), diversity and the P-ratio are shown in this figure.

indicate that Subzone P3A corresponds to the interval from Subzone P3a to the lower part of Subzone P3b of Berggren and Norris (1997) (Figure 7). Hence, the age of Subzone P3A is assigned to the late Paleocene (Selendian).

P3B. *Morozovella acuta*-*Globanomalina pseudomenardii* Interval Subzone

Definition.—The interval of this zone ranges from the FAD of *M. acuta* to the FAD of the *Globanomalina pseudomenardii*.

Occurrence.—This subzone is observed in the interval from Samples ZPW-5 to ZPW-16 in the western section of the Zinda Pir Anticline and from Samples R23 to R28 in the Rakhi Nala (Figures 4, 5).

Correlation and age.—The dominant faunas of this subzone are *Morozovella* forms (*acuta*, *apantesma*, *occlusa*, and *velascoensis*). These species and another three species (*Globanomalina ehrenbergi*, *Igorina pusilla*, and *Subbotina triangularis*) appear first in Sample ZPW-5 of the Zinda Pir west section and R23 of the Rakhi Nala. This

subzone is correlated with the upper part of Subzone P3b of Berggren and Norris (1997), Olsson *et al.* (1999), and with the *P. pusilla pusilla* Zone of Toumarkine and Luterbacher, 1985 (Figure 7). The age of this zone is late Paleocene (Selendian).

P4. *Globanomalina pseudomenardii* Total Range Zone

The total range of *Globanomalina pseudomenardii* (Zone P4) is recognized as an excellent stratigraphic marker in many tropical regions (e.g. Bolli and Krasheninnikov, 1977; Toumarkine and Luterbacher, 1985). In the studied sections, the FAD of *Globanomalina pseudomenardii* has been placed at Sample ZPW-15 in the western section of the Zinda Pir Anticline, and at Sample R25 from the Rakhi Nala (Figures 4, 5). The last appearance datum (LAD) of *G. pseudomenardii* was observed in all three sections. Samples ZPE-20, ZPW-21 of the Zinda Pir Anticline and Sample R32 of the Rakhi Nala show the LAD of *G. pseudomenardii*. Some 25 species belonging to five genera were identified in this zone.

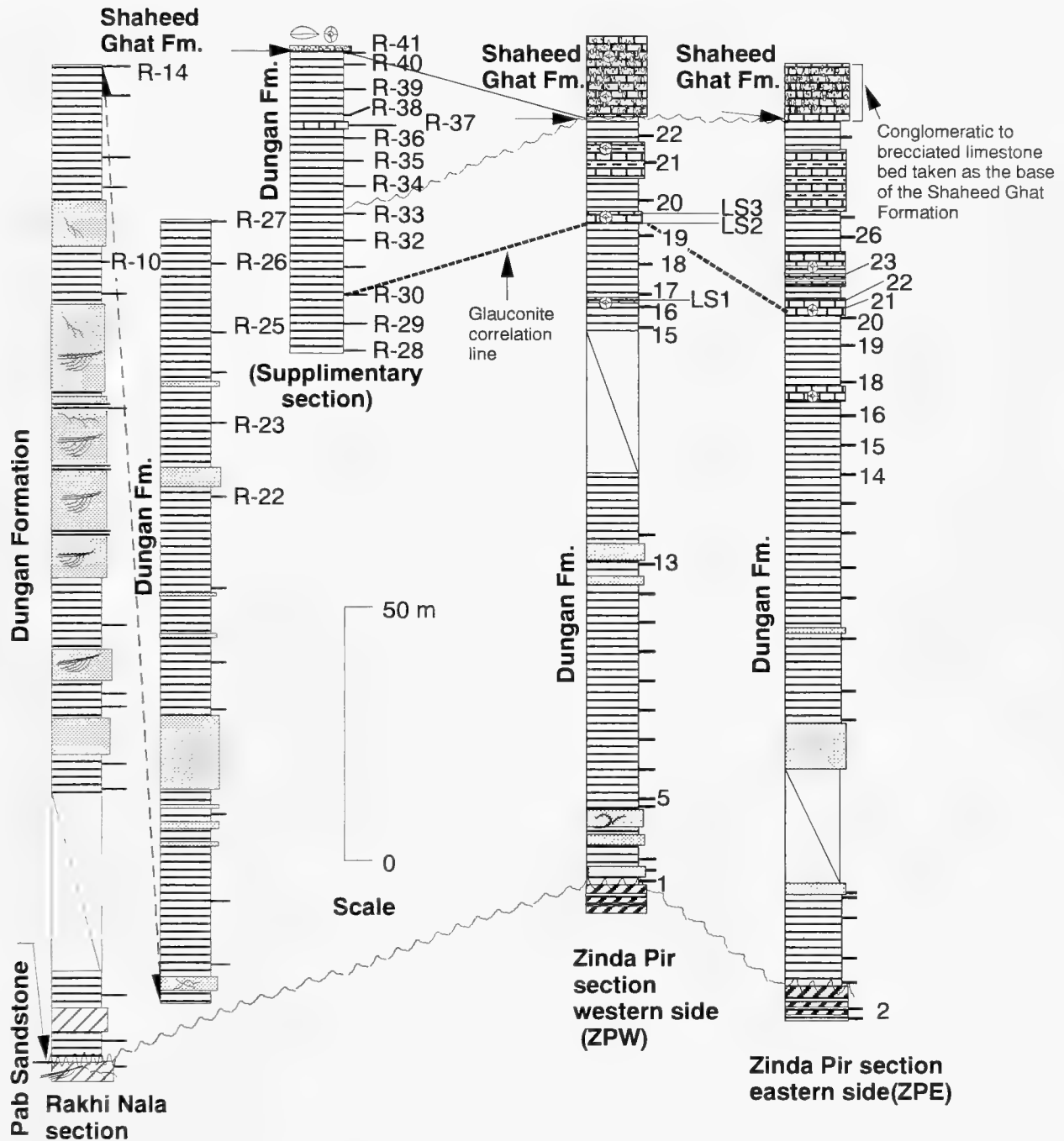


Figure 6. Lithostratigraphic and biostratigraphic correlation between measured columnar sections from the Rakhi Nala and the Zinda Pir area. The numbers indicate the samples containing planktic foraminifers.

Berggren and Norris (1997) have used the FADs of *Acarinina subsphaerica* and *A. soldadoensis soldadoensis* to subdivide their Zone P4 into three subzones (P4a, P4b and P4c). We cannot apply their definition in this area, because the stratigraphic ranges of both *A. subsphaerica* and

A. soldadoensis soldadoensis overlap in the Zinda Pir west section and in the Rakhi Nala (Figures 3–5). Olsson *et al.* (1999) has demonstrated that the stratigraphic range of *Acarinina subsphaerica* may extend upwards, close to Zone P4/P5 boundary. Therefore, we used only the FAD of *A.*

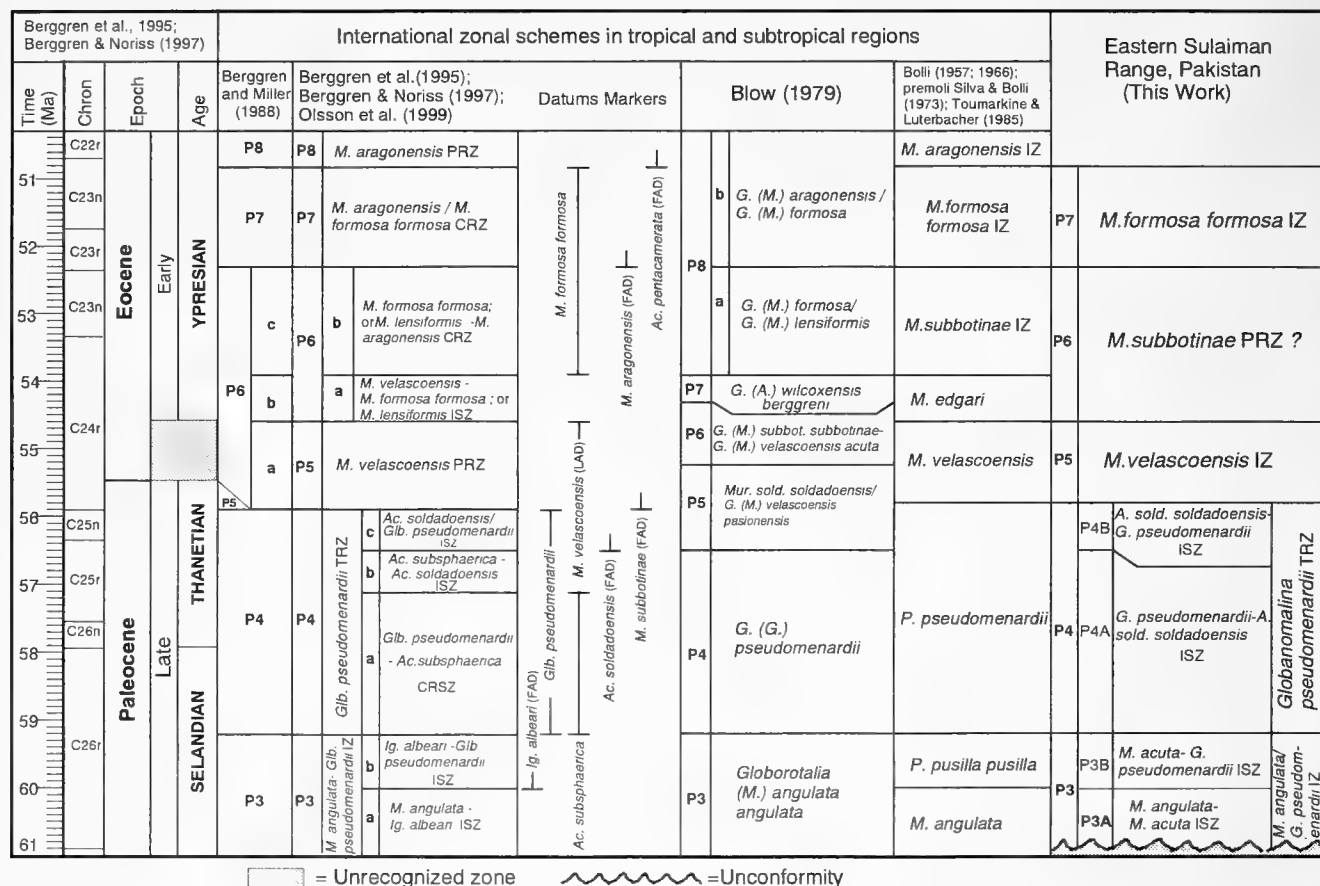


Figure 7. Correlation of planktic foraminiferal zones of the studied area with international low latitude zones. Here IZ: Interval Zone, TRZ: Total Range Zone, PRZ: Partial Range Zone, CRSZ: Concurrent Range Subzone, ISZ: Interval Subzone. A; Ac: *Acarinina*, Glb: *Globanomalina*, Ig: *Igorina*, M: *Morozovella*, P: *Planorotalites*, S: *Subbotina*. Age and epoch boundaries are adopted from Berggren *et al.* (1995) and Berggren and Norris (1997).

soldadoensis soldadoensis as an index marker, and subdivided Zone P4 into two subzones P4A and P4B as follows (Figure 7).

P4A. *Globanomalina pseudomenardii*-*Acarinina soldadoensis soldadoensis* Interval Subzone

Definition.—This subzone is defined as the interval zone between the FAD of *G. pseudomenardii* and the FAD of *A. soldadoensis soldadoensis*.

Occurrence.—This subzone is recognized in both sides of the Zinda Pir Anticline (Samples ZPE-14 to 15 in the east and ZPW-17 to 18 in the west) and in the Rakhi Nala (Samples R25 to R29).

Correlation and age.—The FAD of *A. soldadoensis soldadoensis* is one of the distinctive bioevents in the late Paleocene and is placed at Zones P4a/P4b boundary by Berggren and Norris (1997) and Olsson *et al.* (1999) or within the *Planorotalites pseudomenardii* (= *Globorotalia pseudomenardii*) Zone by Toumarkine and Luterbacher (1985). This subzone corresponds to the joint interval of

P4a and P4b (Figure 7) of Berggren and Norris (1997), and Olsson *et al.* (1999). The age span of this zone is late Paleocene, from the latest Selandian to early Thanetian. In the Dungan Formation, two species of *Igorina* (*albeari*, *pusilla*) and *Parasubbotina varianta* disappear within this subzone.

P4B. *Acarinina soldadoensis soldadoensis*/*Globanomalina pseudomenardii* Concurrent range Subzone

Definition.—Subzone is defined as the interval between the FAD of *A. soldadoensis soldadoensis* and the LAD of *G. pseudomenardii*.

Occurrence.—This subzone ranges from Samples ZPE-15 to 20 in the east section of the Zinda Pir Anticline, ZPW-19 to 21 in the west section of the Zinda Pir Anticline, and R29 to R32 in the Rakhi Nala (Figures 3–5).

Correlation and age.—This subzone is equivalent to Subzone P4c of Berggren and Norris (1997) and Olsson *et al.* (1999). The age of this subzone is late Paleocene (Thanetian). In the Dungan Formation, *Morozovella*

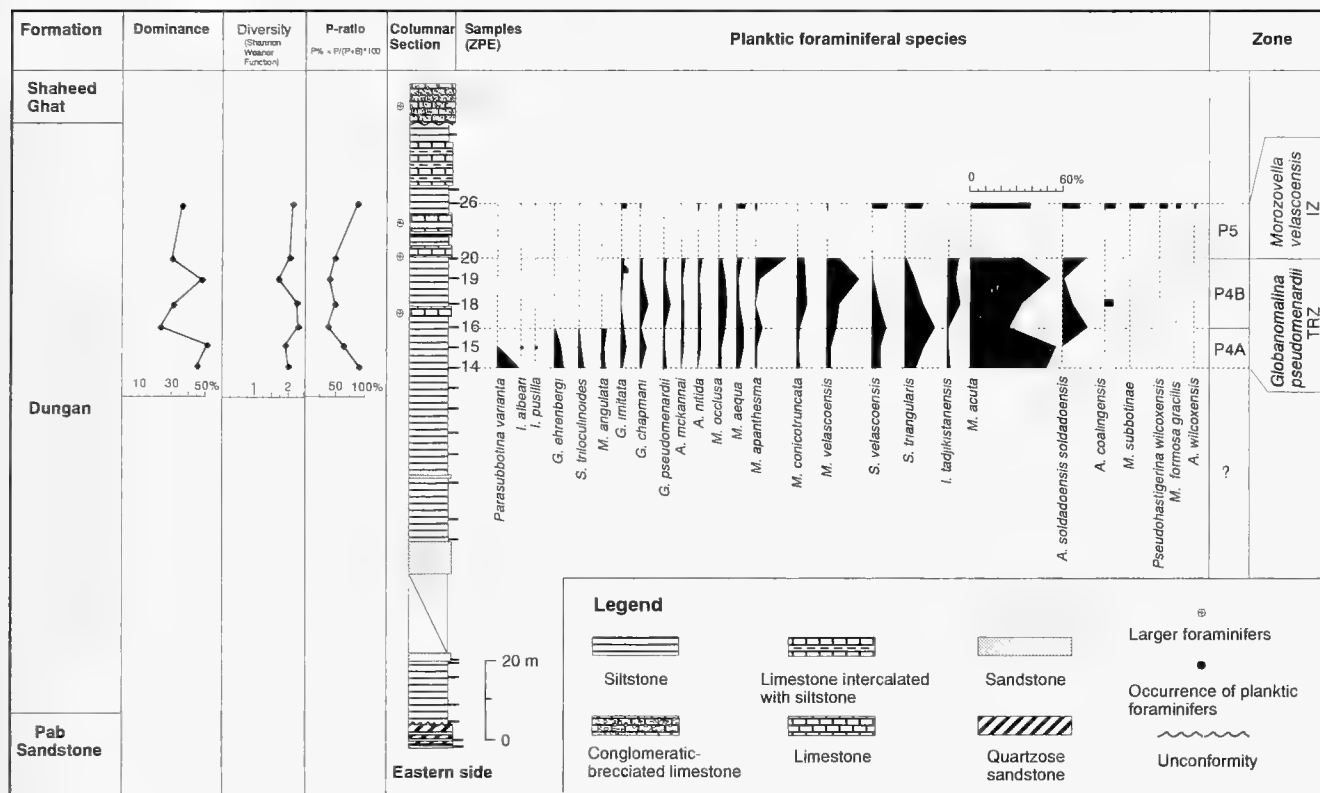


Figure 8. Results of the quantitative analysis of dominance (the most abundant species), diversity, P-ratio and the relative abundances of the characteristic planktic foraminiferal species along the eastern limb of the Zinda Pir Anticline. The numbers indicate the samples containing planktic foraminifers.

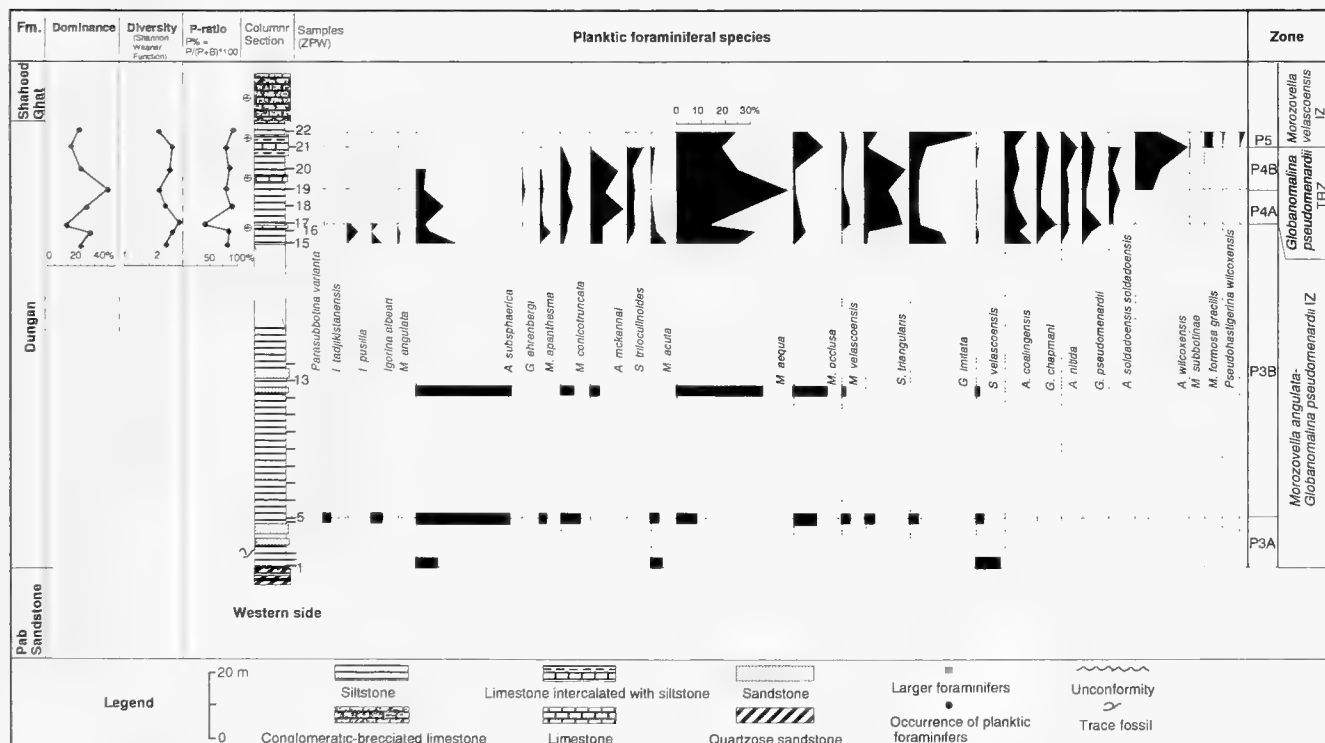


Figure 9. Results of the quantitative analysis of dominance, diversity, P-ratio and relative abundances of the most abundant characteristic planktic foraminiferal species along the western limb of the Zinda Pir Anticline. The numbers indicate the samples containing planktic foraminifers.

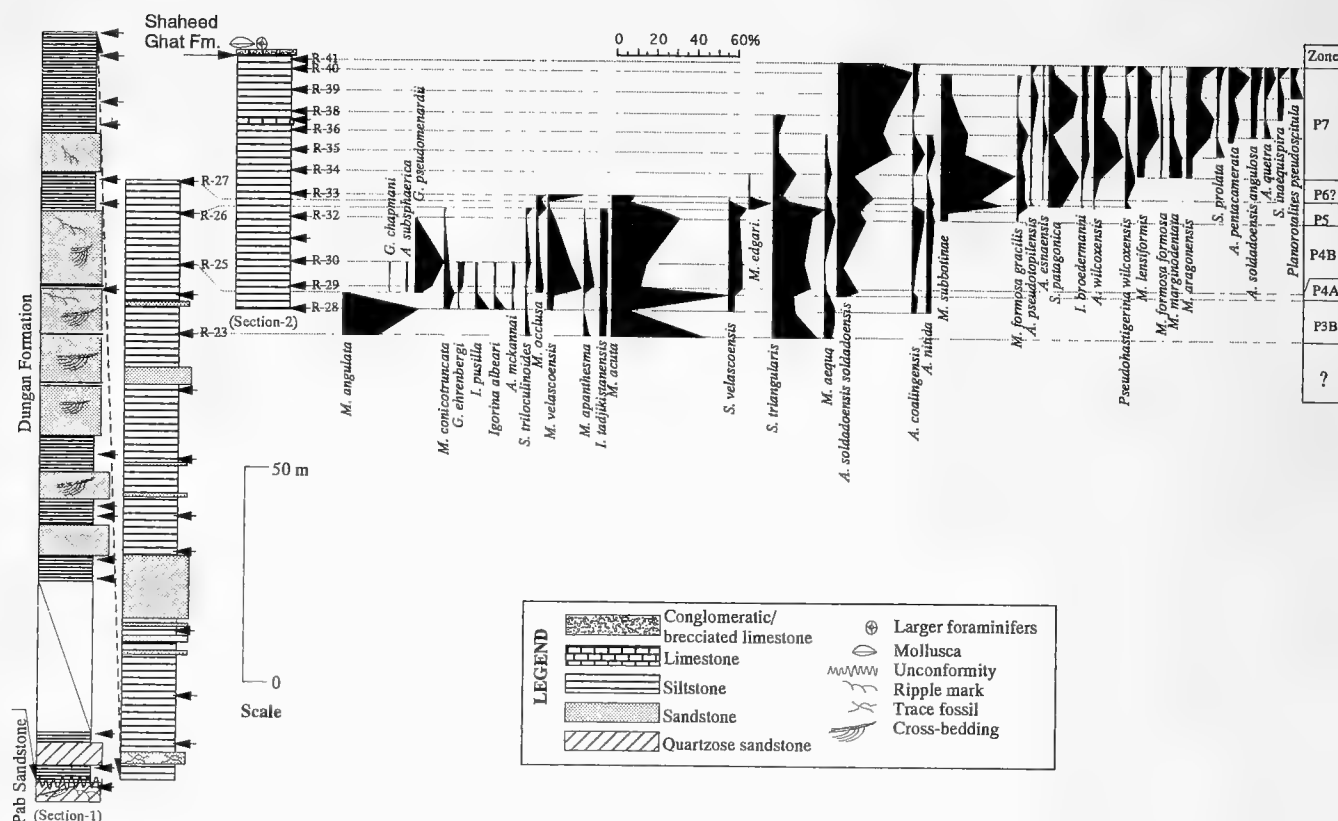


Figure 10. Results of the quantitative analysis of the relative abundances of the most abundant characteristic planktic foraminiferal species from the Rakhi Nala section. The numbers indicate the samples containing planktic foraminifers. For quantitative results of dominance, diversity, and the P-ratio see Figure 5.

angulata and *Globanomalina ehrenbergi* disappear within Subzone P4B.

P5. *Morozovella velascoensis* Interval Zone

Definition.—The definition of Zone P5 is the interval zone between the LAD of *G. pseudomenardii* and the LAD of *Morozovella velascoensis* (e.g. Berggren and Norris, 1997). The base of this zone has been found in all three sections. The upper limit of this zone was placed at the level of Sample R26 in the Rakhi Nala, but its boundary is not clear in the Zinda Pir Anticline, because the hard siltstone of the uppermost part of the Dungan Formation contains no planktic foraminifers (Figures 3, 4).

Occurrence.—This zone ranges from Samples ZPE-20 to 26 in the east and from Samples ZPW-21 to 22 in the west of the Zinda Pir Anticline, and from Sample R32 to R33 in the Rakhi Nala.

Correlation and age.—This zone corresponds exactly to Zone P5 of Berggren and Norris (1997) and Olsson *et al.* (1999). The assemblages of planktic foraminifers in the Dungan Formation contain abundant index species of latest Paleocene to early Eocene age such as *Morozovella subbotinae*, *M. formosa gracilis*, *Acarinina wilcoxensis* and *Pseudohastigerina wilcoxensis*. In particular, the last species is a marker for recognizing the Paleocene/Eocene (P/E)

boundary, appearing first just above the P/E boundary (Berggren, 1969; Stainforth *et al.*, 1975; Berggren and Aubry, 1998). The FAD of this species has been recorded in Samples ZPW-21 and ZPE-26 in the Zinda Pir, and in Sample R27 in the Rakhi Nala.

The chemo- and biostratigraphic events of a negative excursion of $\delta^{13}\text{C}$ (CIE) and the benthic foraminiferal extinction event (BEE) are used as the P/E boundary markers by many workers (e.g. Berggren and Aubry, 1998; Berggren *et al.*, 1998). The BEE in the investigated area is recognized between Samples R32 and R33 of the Rakhi Nala section (personal communication by Riisuo Nomura, Shimane University, Japan). Hence, the P/E boundary can be placed between Samples R27 and R26 in the Rakhi Nala section. The P/E boundary in the Zinda Pir sections can be drawn tentatively between the Samples ZPE-20 and 26 in the east and ZPW-21 and 22 in the west, respectively. The age of this zone ranges from the latest Paleocene to earliest Eocene.

Eocene Zones of the Dungan Formation

In the study area, the siltstone sequence of the Dungan Formation is overlain by the conglomeratic to brecciated limestone beds present in the basal part of the Shaheed Ghat Formation. This field observation implies an

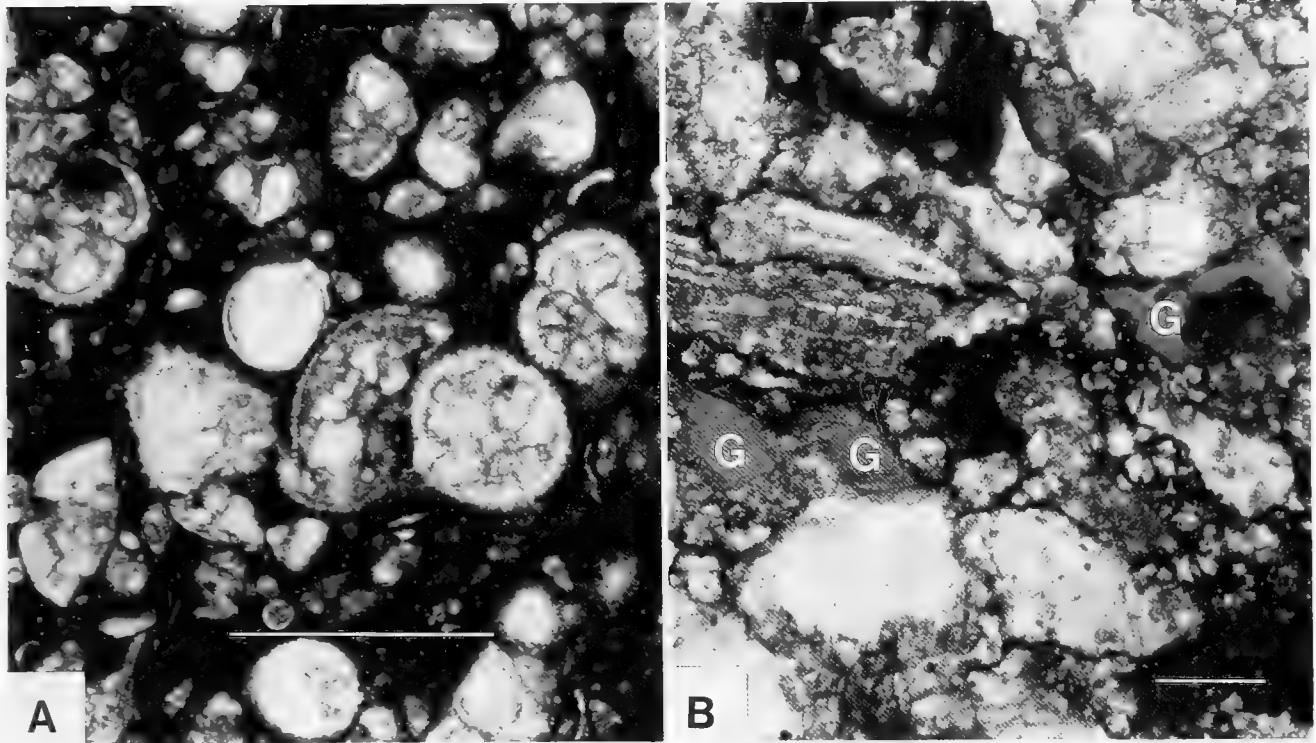


Figure 11. **A.** Pelagic limestone (wackestone) containing abundant planktic foraminifers from the Rakhi Nala section, Sample R37 (scale bar = 0.5mm). **B.** Limestone (wackestone) showing squashed (compacted) larger foraminifers and glauconitic grains from the Zinda Pir western section, Sample LS3 (scale bar = 0.5mm). G stands for glauconite grain.

unconformable relationship between the two formations. The biostratigraphic data from the Dungan Formation supports this interpretation because the age of the siltstone beds in the uppermost part of the Dungan Formation in the Zinda Pir sections is latest Paleocene to earliest Eocene (Zone P5), whereas such beds in the Rakhi Nala section are early Eocene in age (Zone P7). Two early Eocene zones described here are recognized from the Rakhi Nala section.

P6. *Morozovella subbotinae* Partial Range Zone

Definition.—This zone is defined as an interval zone between the LAD of *M. velascoensis* and the FAD of *M. aragonensis*.

Occurrence.—None occurred in the intervening samples between the Sample R27 and the Sample R34 in the study area.

P7. *Morozovella aragonensis*/*M. formosa formosa* Concurrent-Range Zone

Definition.—This zone is defined by the interval from the FAD of *M. aragonensis* to the LAD of *Morozovella formosa formosa*. The upper boundary of this zone probably lies within the overlying Shaheed Ghat Formation.

Occurrence.—The interval of this zone is recognized between the Samples R34 and R41 that include many early Eocene species such as *Morozovella aragonensis*, *M.*

formosa formosa, *Subbotina inaequispira*, and *S. lozanoi*. Two species (*Acarinina nitida* and *Morozovella aequa*) disappear close to the top of this interval (Figure 5).

Correlation and age.—Zone P7 of Blow (1969, 1979) has been revised by Berggren and Miller (1988), who used the FAD of *M. aragonensis* as the lower boundary of this zone and the LAD of *M. formosa formosa* as the top. This zone corresponds to the joint interval of the *M. formosa formosa* Zone and the lower part of the *Acarinina pentacamerata* Zone of Toumarkine and Luterbacher (1985). The age of this zone is early Eocene (middle to late Ypresian).

Quantitative analysis of planktic assemblages

For calculation of quantitative indices (plankton ratio, dominance and species diversity), we used the samples containing over 100 individuals. In the Rakhi Nala, all samples from Zone P3 to P7 yielded abundant and well-preserved foraminifers (Appendix 2). However, the total number per samples of individuals recovered from Zone P3 of the Zinda Pir sections amounted to less than 100. The number of specimens in the other samples in the Zinda Pir exceeded 200 individuals per sample.

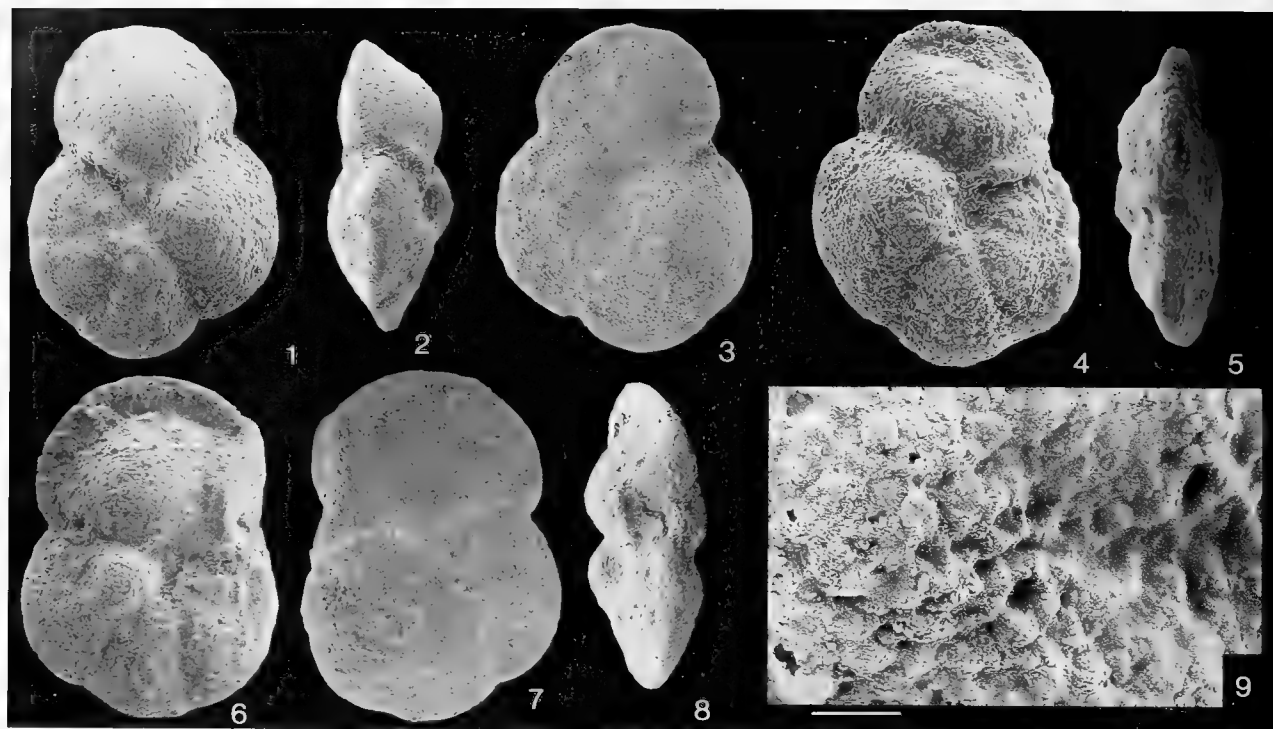


Figure 12. *Globanomalina rakhiensis* sp. nov. 1–3: Holotype, (IGUT coll. cat. no. 50101) umbilical, side and spiral views, Sample R41, all $\times 270$. 4, 5: Paratype, (IGUT coll. cat. no. 50102), umbilical and side views, Sample R41, all $\times 330$. 6–8: Paratype, (IGUT coll. cat. no. 50103) side, spiral and umbilical views. This specimen has more compressed peripheral margin on umbilical side, more limbate intercameral sutures on spiral side and more developed keel in side view, Sample R41, all $\times 300$. 9: An enlarged view of specimen (as illustrated in Figure 4) shows smooth wall surface with some pustules (scale bar = 10 μm)

Results and discussion

1. Plankton-ratio

The plankton-ratio (P-ratio) is expressed by the following formula:

$$\text{P-ratio} = [P/(P+B)] \times 100$$

Here P and B represent the number of specimens of planktic and benthic foraminifers, respectively. The trend of P-ratios differs between the eastern and western sections of the Zinda Pir Anticline (Figures 8, 9). In the east, the P-ratios of Zone P4A are as high as 90%, decreasing gradually to a minimum (39%) in Zone P4B, and then recovering to 89% in Zone P5. In the west, the P-ratios are consistently high (80–90%) during Zones P3B to P5, except for a figure of 31% in Sample ZPW-17 in the lowermost part of Zone P4A. In the Rakhi Nala section, the P-ratios of all samples show high values of more than 95% (Figure 5).

2. Species compositions

The morozovellid species are common to abundant throughout the studied sequences, exceeding about 30–40% of the total number of specimens (Figures 8–10). The dominant morozovellids are *M. angulata* in Zone P3B, *M. acuta* and *M. velascoensis* in Zone P4 and three species (*M.*

acuta, *M. subbotinae*, and *M. aequa*) in Zone P5 in the Zinda Pir area. In the Rakhi Nala region, the assemblage of Zone P3B is dominated by *M. acuta* and *M. angulata* (40–60%), whereas that of Zones P4 and P5 is dominated by *M. acuta*, *M. conicotruncata*, *M. occlusa*, and *M. velascoensis* (30–35%). The relative abundance of *Acarinina* and *Subbotina* during Zones P3 to P5 is relatively high, fluctuating between 10 and 20% of the total for each genus. Those of the other genera (*Igorina*, *Globanomalina*, and *Parasubbotina*) are less than 10% for each genus.

The replacement of the Paleocene morozovellid group (*M. velascoensis*, *M. angulata*, *M. conicotruncata* and *M. apantesma*) by early Eocene forms (*M. formosa gracilis*, *M. formosa formosa*, *M. lensiformis*, *M. subbotinae*, *M. marginodentata* and *M. edgari*) occurred during Zones P5 to P6 (Figure 5). The acarininids (*A. pentacamerata*, *A. soldadoensis soldadoensis*, *A. wilcoxensis*) and subbotinids (*S. patagonica*, *S. inaequispira*, *S. prolata*) increased within Zone P7, accompanied by a decrease in the abundances of the morozovellid forms (Figure 10). This increase in the abundance of acarininid and subbotinid forms is probably related to a temperature decrease after the Paleocene-Eocene boundary. In the late Paleocene, the period spanning latest zone P4 to P5 is of maximum warmth (LPTM), with Zones

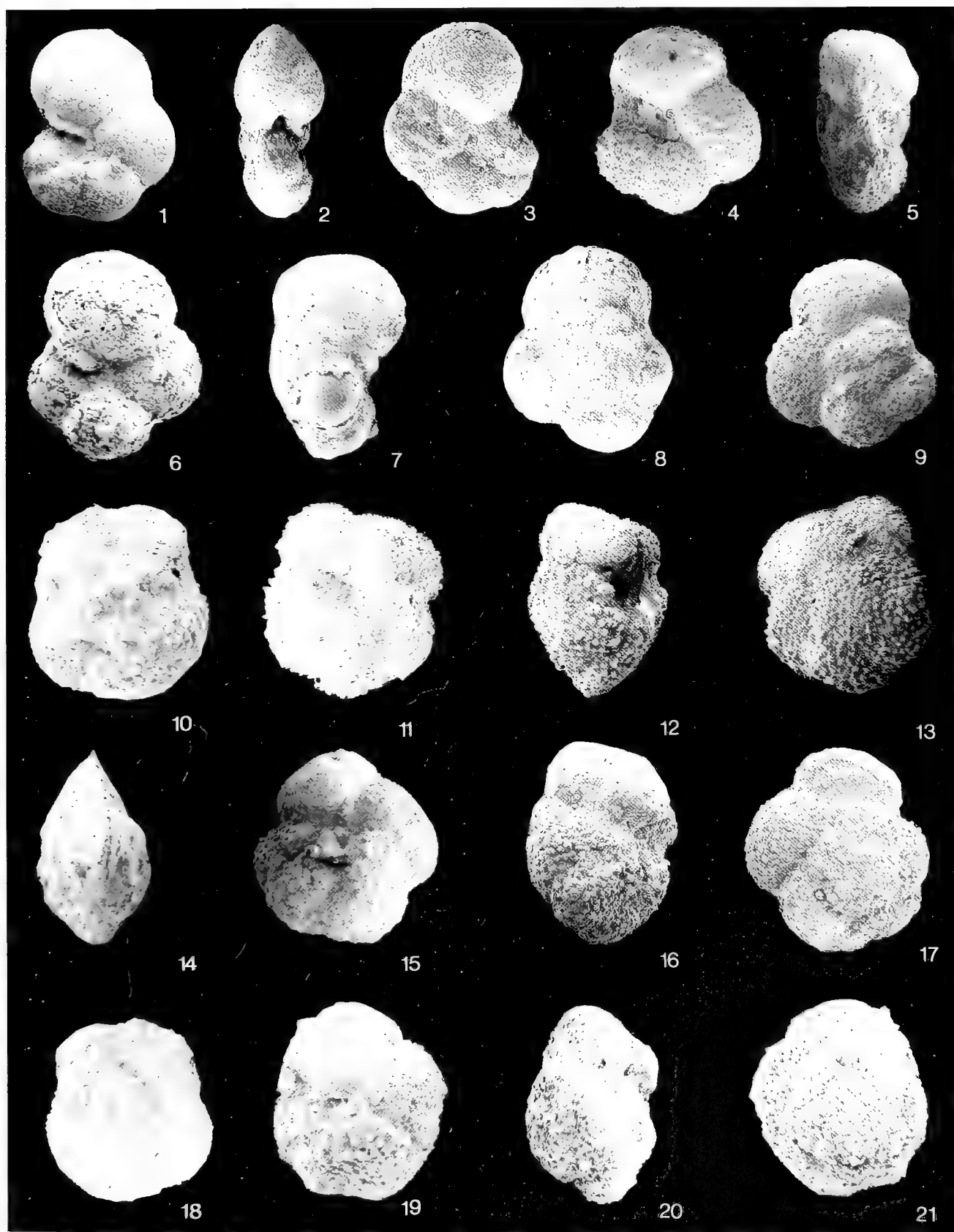


Figure 13.

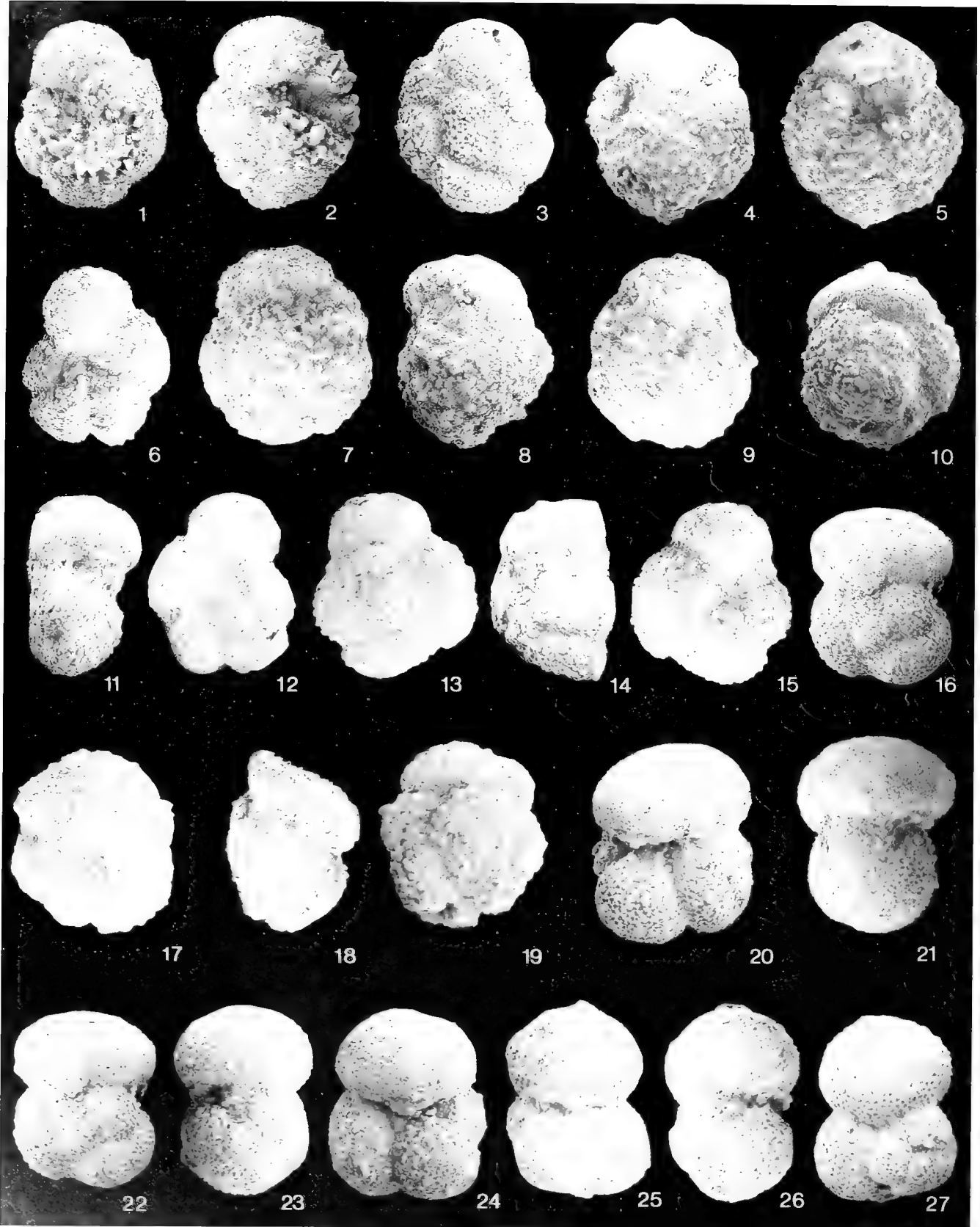


Figure 14.

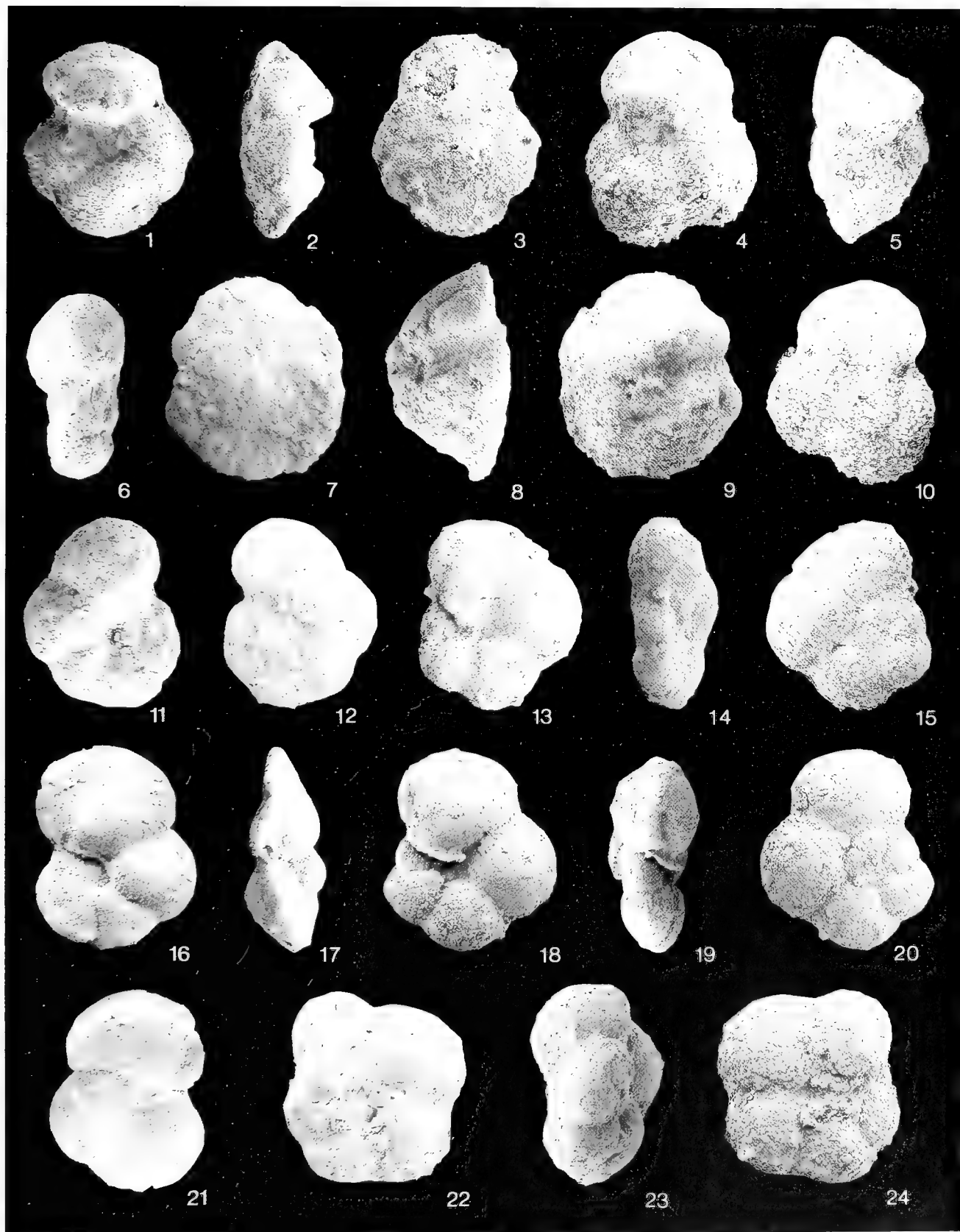


Figure 15.

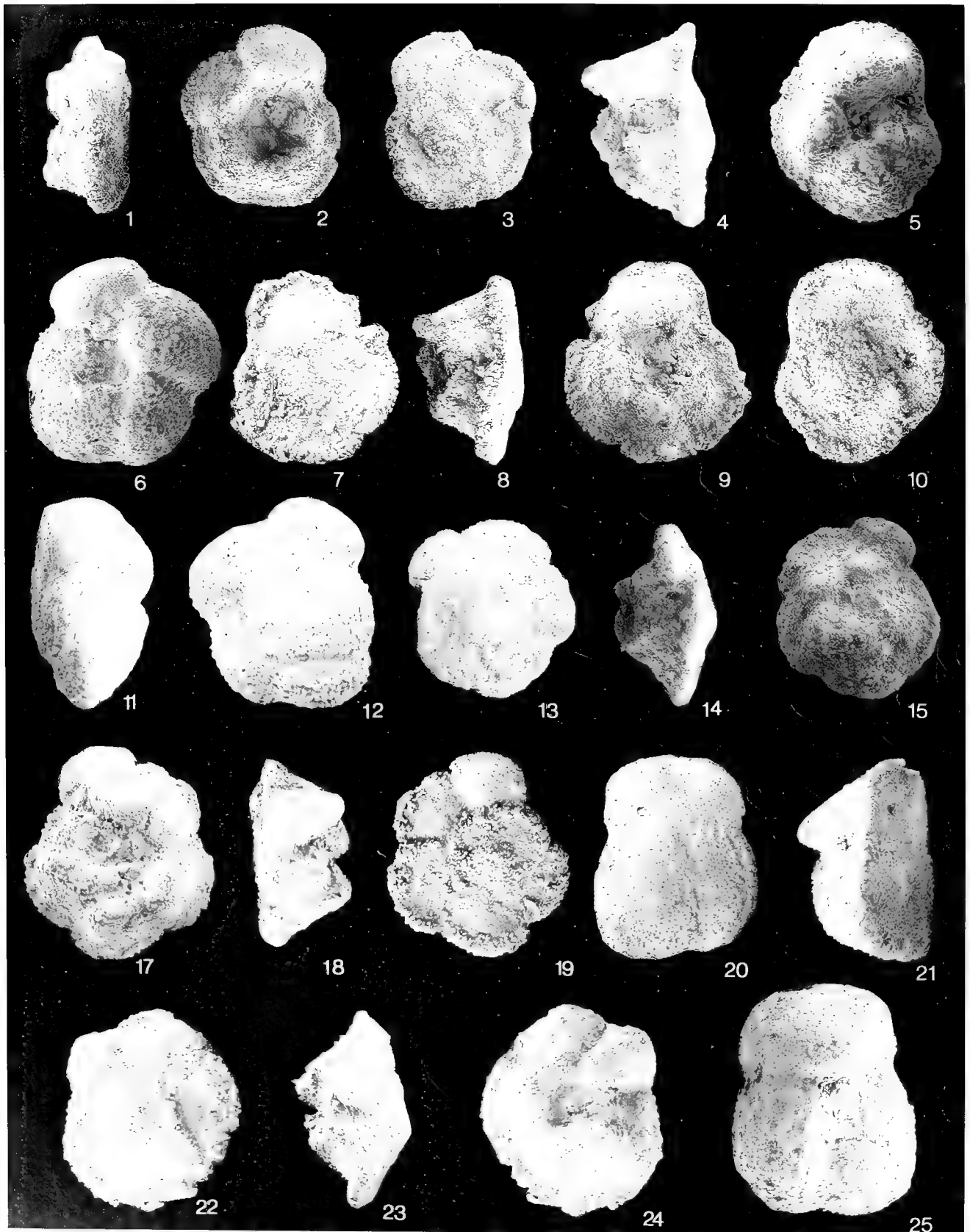


Figure 16.

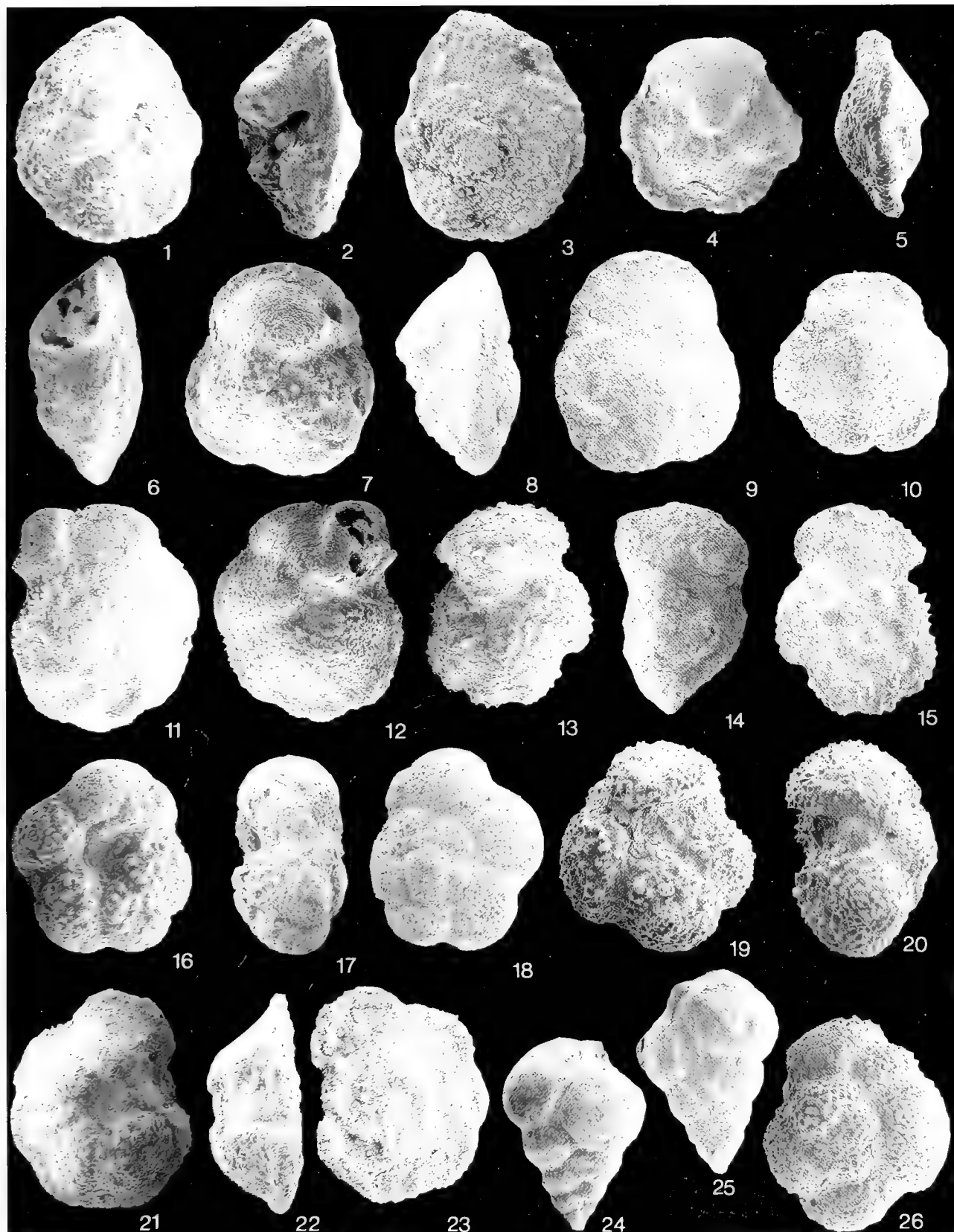


Figure 17.

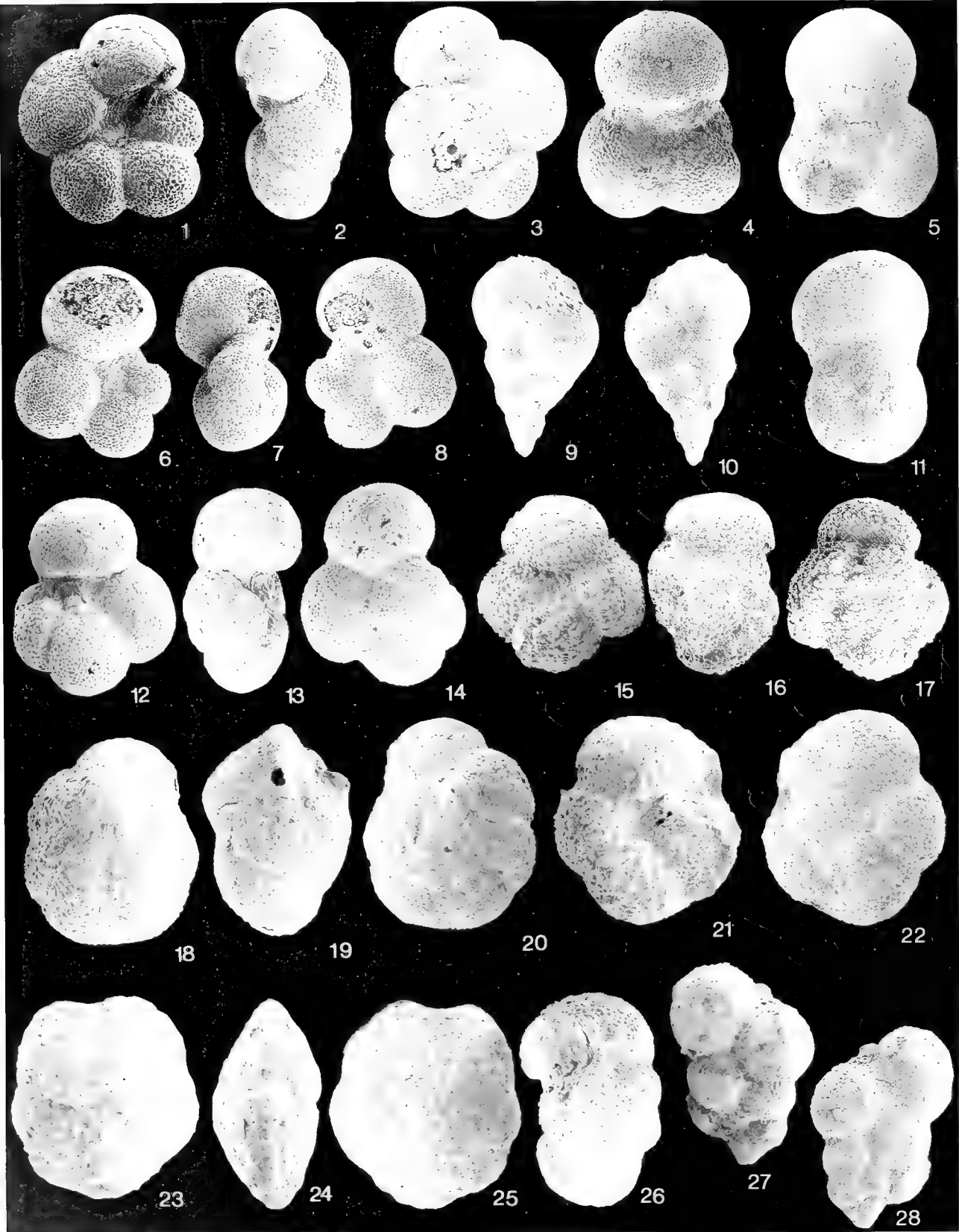


Figure 18.

P6b and P7 becoming slightly cooler (e.g., Stott *et al.*, 1990; Bralower *et al.*, 1995). This cooling event is probably responsible for the increase in percentage of *Acarinina* and *Subbotina* species in Zone P7.

3. Diversity and dominance trends

We calculated the species diversity in both sections of the Zinda Pir (Zones P3B to P5) and in the Rakhi Nala section (Zones P3 to P7) using the Shannon-Wiener Function by the following mathematical expression.

$$H(S) = -\sum_{i=1}^S p_i \ln p_i \text{ (from } i = 1 \text{ to } S)$$

Where p_i is the relative abundance of the i -th species in a

sample and S is the number of species. Dominance index is expressed as percentages of the most abundant species. The relationship between the Shannon-Wiener diversity index and dominance index display distinct opposite trends (Figures 8–10).

In the east of the Zinda Pir, the species richness decreases gradually from 20 to 15 species during Zones P4A to P5 (Appendix 2). The diversity index is, however, relatively constant (1.9 and 2.0), with generally lower values than in the western samples. The lowest value (15 species) was recorded from the earliest Eocene Sample ZPE-26, but this figure is not the overall minimum (Figure 8).

Figure 13. (p.287) 1–3. *Globanomalina chapmani* (Parr), umbilical, side and spiral views, Sample ZPW-17, all $\times 250$. 4, 5, 9. *Acarinina wilcoxensis* (Cushman and Ponton), umbilical, side and spiral views, Sample ZPW-21, all $\times 230$. 6–8. *Parasubbotina varianta* (Subbotina), umbilical, side and spiral views, Sample ZPW-5, all $\times 500$. 10, 14, 18. *Igorina albeari* (Cushman and Bermudez), umbilical, side and spiral views, Sample ZPW-15, all $\times 230$. 11–13. *Igorina tadjikistanensis* (Bykova), umbilical, side and spiral views, Sample ZPW-17, all $\times 220$. 15–17. *Acarinina strabocella* (Loeblich and Tappan), umbilical, side and spiral views, Sample ZPW-16, all $\times 230$. 19–21. *Igorina pusilla* (Bolli), umbilical, side and spiral views, Sample ZPW-17, all $\times 300$.

Figure 14. (p.288) 1–3. *Acarinina mckannai* (White), umbilical, side and spiral views, Sample ZPW-17, all $\times 180$. 4–5, 10. *Acarinina nitida* (Martin), side, umbilical and spiral views, Sample ZPW-20, all $\times 220$. 6, 11–12. *Acarinina soldadoensis soldadoensis* (Bronnimann), umbilical, side and spiral views, Sample ZPW-20, all $\times 170$. 13–15. *Acarinina soldadoensis soldadoensis* (Bronnimann) spiral, side and umbilical views, Sample ZPW-20, all $\times 200$. 7–9. *Acarinina subsphaerica* (Subbotina), spiral, side and umbilical views, Sample ZPW-19, all $\times 220$. 16, 20, 21. *Subbotina velascoensis* (Cushman), spiral, umbilical and side views, Sample ZPW-17, all $\times 200$. 17–19. *Acarinina coalingensis* (Cushman and Hanna), umbilical, side and spiral views, Sample ZPW-20, all $\times 200$. 22–24. *Subbotina triangularis* (White), spiral, side and umbilical views, Sample ZPW-17, all $\times 180$. 25–27. *Subbotina triloculinoidea* (Plummer), umbilical, side and spiral views, Sample ZPW-17, all $\times 300$.

Figure 15. (p.289) 1–3. *Morozovella angulata* (White), umbilical, side and spiral views, Sample ZPE-15, all $\times 150$. 4, 5, 10. *Morozovella subbotinae* (Morozova), umbilical, side and spiral views, Sample ZPE-26, all $\times 150$. 6, 11, 12. *Pseudohastigerina wilcoxensis* (Cushman and Ponton), apertural face, lateral views, Sample ZPW-22, all $\times 270$. 7–9. *Morozovella conicotruncata* (Subbotina), spiral, side and umbilical views, Sample ZPW-16, all $\times 200$. 13–15. *Globanomalina imitata* (Subbotina), umbilical, side and spiral views, Sample ZPW-18, all $\times 250$. 16, 17, 21. *Globanomalina pseudomenardii* (Bolli), umbilical, side and spiral views, Sample ZPW-17, all $\times 170$. 18–20. *Globanomalina ehrenbergi* (Bolli), umbilical, side and spiral views, Sample ZPW-17, all $\times 170$. 22–24. *Globanomalina imitata* (Subbotina), spiral, side and umbilical views, Sample ZPW-18, all $\times 200$.

Figure 16. (p.290) 1–3. *Morozovella acuta* (Toulmin), side, umbilical and spiral views, Sample ZPW-17, all $\times 100$. 4–5, 10. *Morozovella acuta* (Toulmin), side, umbilical and spiral views, Sample ZPW-19, all $\times 160$. 6, 11, 12. *Morozovella apantesma* (Loeblich and Tappan), umbilical, side and spiral views, Sample ZPW-21, all $\times 200$. 7–9. *Morozovella acutispira* (Bolli and Cita), spiral, side and umbilical views, Sample ZPW-15, all $\times 150$. 13–15. *Morozovella gracilis* (Bolli), spiral, side and umbilical views, Sample ZPE-26, all $\times 130$. 17–19. *Morozovella velascoensis* (Cushman), umbilical, side and spiral views, Sample ZPE-15, all $\times 140$. 20, 21, 25. *Morozovella aequa* (Cushman and Renz), spiral, side and umbilical views, Sample ZPW-21, all $\times 220$. 22–24. *Morozovella occlusa* (Loeblich and Tappan), spiral, side and umbilical views, Sample ZPW-15, all $\times 160$.

Figure 17. (p.291) 1–3. *Morozovella edgari* (Primoli Silva and Bolli), umbilical, side and spiral views, Sample R33, all $\times 270$. 4, 5, 10. *Morozovella marginodentata* (Subbotina), umbilical, side and spiral views, Sample R40, all $\times 200$. 6, 11, 12. *Morozovella aragonensis* (Nuttall), side, spiral and umbilical views, Sample R41, all $\times 130$. 7–9. *Morozovella lensiformis* (Subbotina), umbilical, side and spiral views, Sample R40, all $\times 170$. 13–15. *Acarinina quetra* (Bolli), umbilical, side and spiral views, Sample R41, all $\times 180$. 16–18. *Acarinina pentacamerata* (Subbotina), umbilical, side and spiral views, Sample R40, all $\times 150$. 19, 20, 26. *Acarinina soldadoensis angulosa* (Bolli), umbilical, side and spiral views, Sample R38, all $\times 200$. 21–23. *Morozovella formosa formosa* (Bolli), umbilical, side and spiral views, Sample R41, all $\times 130$. 24, 25. *Chiloguembelina trinitatis* (Cushman and Renz), lateral views, Sample R30, all $\times 350$.

Figure 18. (p.292) 1–3. *Subbotina lozanoi* (Colom), umbilical, side and spiral views, Sample R41, all $\times 170$. 4, 5, 11. *Subbotina patagonica* (Todd and Knicker), umbilical, spiral and side views, Sample R38, all $\times 150$. 6–8. *Subbotina inaequispira* (Subbotina), umbilical, side and spiral views, Sample R41, all $\times 150$. 9–10. *Chiloguembelina crinita* (Glaessner), lateral views, Sample R30, all $\times 370$. 12–14. *Subbotina prolata* (Bolli), umbilical, side and spiral views, Sample R41, all $\times 170$. 15–17. *Acarinina pseudotopilensis* (Subbotina), umbilical, side and spiral views, Sample R39, all $\times 160$. 18–20. *Igorina broedermanni* (Cushman and Bermudez), umbilical, side and spiral views, Sample R41, all $\times 200$. 21, 22, 26. *Acarinina esnaensis* (LeRoy), umbilical, spiral and side views, Sample R41, all $\times 190$. 23–25. *Planorotalites pseudoscitula* (Glaessner), umbilical, side and spiral views, Sample R39, all $\times 450$. 27, 28. *Chiloguembelina wilcoxensis* (Cushman and Ponton), lateral views, Sample R33, all $\times 180$.

In the western section, the species richness during Zones P3B to P4 is consistently high (17 to 20 species), except for sample ZPW-18 (Zone P4A, 16 species) (Appendix 3). The species diversity fluctuates between 2.1 and 2.6. The minimal values of both richness (15 species) and diversity (2.1) are yielded by the earliest Eocene Sample ZPW-22 (Figure 9).

In the Rakhi Nala section, the species richness during the Paleocene (Zones P3B to P4) is high and nearly constant (19 to 22 species), excepting Sample R23 (8 species, Zone P3B). The diversity of two samples (Samples R23 and R25) of Zone P3B-P4 is about 1.6 but varies to 2.5 in Sample R30 (Zone P4B). The Eocene species richness during Zones P5 to P7 ranges from 16 to 20 species, and the diversity index is constant at close to 2.5 (Figure 10). The diversity during the earliest Eocene is consistently high (2.2–2.3), differing from the trends in the Zinda Pir.

4. Depositional environment

The sequence of the Dungan Formation is characterized by a remarkable change of lithology in the studied regions. During the late Paleocene (Zone P3), the strata of both regions (Zinda Pir and Rakhi Nala) consist of siltstone subordinate to sandstone. The interbeds of sandstone show the westward-thickening trend as sandstone beds are abundant and thick in the Rakhi Nala (Figure 6). In Zone P4, two basins were filled with siltstone, with rarely intercalating thin limestone beds containing larger foraminifers. After Zone P5, the limestones became thicker in the eastern section of the Zinda Pir, and the lithology changed from a siltstone-dominant facies to a limestone-dominant one in the eastern area. As a whole, limestone deposits thinned to the westward from the Zinda Pir to the Rakhi Nala, while siltstone deposition went on in the Rakhi Nala basin, located in the western region.

As a rule, plankton-ratios (P-ratios) increase from the shelf to the open-ocean environment, and exceed 50% in the deeper environment beyond the outer shelf in both modern and ancient sediments (e.g. Ingle, 1980; Gibson, 1989). The high P-ratios of all three sections of the Dungan Formation strongly indicate an open marine environment in the studied area. The highest P-ratios (98 to 99%), high values of species richness and diversity index in the Rakhi Nala suggest that the paleodepth of the Rakhi Nala basin was greater than that of the Zinda Pir. Furthermore, the planktic foraminiferal assemblage of the western section in the Zinda Pir Anticline also represents higher species richness and P-ratios than does that of the eastern one. Hence, the sedimentary basin of the Dungan Formation, as a whole, is thought to constitute a continental slope dipping from east to west.

The westward-deepening basin is ascertained by lithological evidence, as mentioned above, namely, that the thickness of the limestone beds intercalated with the Paleocene siltstone in the Zinda Pir area are thinner in the western section than in the eastern ones (Figure 6). Moreover, petrographic studies of these intercalated limestones from the Rakhi Nala show an abundant pelagic faunas (Figure 11A), while some limestone bands from the Zinda Pir area contain deformed or broken specimens of

larger foraminifers along with many glauconite grains (Figure 11B), indicating a shallow marine environment. Actually, these thin limestone bands are of turbidite origin and were emplaced in the deep-water siltstone sequence, possibly due to unstable tectonics in tectonic episodes. Our interpretation is also supported by Humayon *et al.* (1991), who have reported the westward-deepening-basin structure of the Sulaiman fold belts using seismic reflections and drilling core data.

Conclusions

Five biostratigraphic zones P3 to P7 of the tropical zones were recognized in the Dungan Formation exposed in the eastern Sulaiman Range. Zones P3 and P4 are subdivided into two subzones (Subzones A and B). The Dungan Formation is assigned to the late Paleocene to early Eocene. Based on quantitative analysis of planktic species of P-ratios, species richness and species diversity, the Dungan Formation is thought to have been deposited in a relatively deep-water environment, forming a westward-dipping continental slope during the late Paleocene to early Eocene.

Systematic description

Superfamily Rotaliporaceae Sigal, 1958

Family Hedbergellidae Loeblich and Tappan, 1961

Genus *Globanomalina* Haque 1956

Globanomalina rakhiensis sp. nov.

Figure 12

Description.—Test very small, spiral side flat to slightly convex, umbilical side low convex; equatorial periphery elongate, distinctly lobulate; peripheral margin acute, strongly to moderately compressed with a keel; 14 or 15 chambers arranged in 3 whorls, all visible from spiral side; commonly five (rarely six) chambers in the last whorl increase very rapidly in size; on umbilical side intercameral sutures depressed and weakly curved whereas strongly recurved and limbate on spiral side; surface finely perforate; umbilicus narrow and shallow; aperture low arch-shaped, interiomarginal, umbilical-extraumbilical with distinct lip.

Type and material.—Holotype, IGUT (Institute of Geosciences, University of Tsukuba) coll. cat. no. 50101, from Sample R41, Dungan Formation, Rakhi Nala section, maximum diameter 0.27 mm, width 0.20 mm. Paratype, IGUT coll. cat. no. 50102, Sample R41, Dungan Formation, Rakhi Nala section, maximum diameter 0.27 mm, width 0.20 mm. Paratype, IGUT coll. cat. no. 50103, Sample R41, Dungan Formation, Rakhi Nala section, maximum diameter 0.26 mm, width 0.21 mm.

Remarks.—The species is common in Sample R41. The largest specimen is 0.27 mm in diameter, but specimens are usually less than 0.15 mm. *Globanomalina rakhiensis* sp. nov. is a small but very distinctive species and might have been overlooked previously due to its small size. It can be missed if using the 150 µm size fraction. This species shows variation in size and degree of compression of the peripheral margin. The holotype (Figure 12.1–12.3) is less

compressed than the paratype (Figure 12.6 – 12.8). *Planorotalites pseudoscutula* (Glaessner, 1937) is very similar to *G. rakhiensis* sp. nov. but differs in having more chambers in the last whorl (6 or 7) and a circular periphery, and in being more lenticular.

Globanomalina rakhiensis sp. nov. is a homeomorph of the late Paleocene *Globanomalina pseudomenardii* (Bolli, 1957) as both forms possess a compressed planoconvex test, 5 chambers in the last whorl, and a low-arched umbilical-extraumbilical aperture that bears a lip. *G. rakhiensis* sp. nov. is easily distinguished from *G. pseudomenardii* by its small size and relatively weak keel.

The stratigraphic range of *G. pseudomenardii* is restricted to Zone P4 (late Paleocene) in many works (Toumarkine and Luterbacher, 1985; Berggren and Miller, 1988, Berggren *et al.*, 1995; Berggren and Norris, 1997; Olsson *et al.*, 1999, etc). However, Blow (1979) extended the age range of this species to his Zone P7 (early Eocene). We suggest that *Globorotalia* (*G.*) *pseudomenardii* identified by Blow (1979) from his Zone P7 (pl. 111, figs. 1–4; pl. 112, figs. 2, 3; 9–10) is quite similar to our new species (*G. rakhiensis*). Therefore, he might have misidentified *G. rakhiensis* sp. nov.

This new species is named after a local river, Rakhi Nala, along which this section is exposed.

Stratigraphic range.—*Globanomalina rakhiensis* sp. nov. yielded by Sample R41 is assigned to the *M. formosa* Zone (P7), corresponding to Zone P7 of Berggren and Miller (1988) and Berggren *et al.* (1995). Therefore, the stratigraphic range of this species is within the middle lower Eocene.

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Appendix 1: Faunal reference list

The classification of the planktic foraminifera adopted in this paper is based on Berggren *et al.* (1995), Berggren and Norris (1997) and Olsson *et al.* (1999). The synonymies of the planktic foraminifers are restricted to original descriptions. The SEM photographs of marker species are presented in Figures 13 to 18.

- Acarinina coalingensis* (Cushman and Hanna) (Figure 14.17–14.19)
Globigerina coalingensis Cushman and Hanna, 1927, p. 205, pl. 14, fig. 4.
Acarinina esnaensis (LeRoy) (Figure 18.21, 18.22, 18.26)
Globigerina esnaensis LeRoy, 1953, p. 31, pl. 6, figs. 8–10.
Acarinina mckannai (White) (Figure 14.1–14.3)
Globigerina mckannai White, 1928, p. 194, pl. 27, figs. 16a–c.
Acarinina nitida (Martin) (Figure 14.4–14.5, 14.10)
Globigerina nitida Martin, 1943, p. 115, pl. 7, figs. 1a–c.
Acarinina quetra (Bolli) (Figure 17.13–17.15)
Globorotalia quetra Bolli, 1957, p. 79–80, pl. 19, figs. 1–6.
Acarinina pentacamerata (Subbotina) (Figure 17.16–17.18)
Globorotalia pentacamerata Subbotina, 1947, p. 128–129, pl. 12–17, figs. 24–26.
Acarinina pseudotopilensis Subbotina (Figure 18.15–18.17)
Acarinina pseudotopilensis Subbotina, 1953, p. 227–228, pl. 21, figs. 13.
Acarinina soldadoensis angulosa (Bolli) (Figure 17.19–17.20, 17.26)
Globigerina soldadoensis angulosa Bolli, 1957, p. 71, pl. 16, figs. 46.
Acarinina soldadoensis soldadoensis (Bronnimann) (Figure 14.6, 14.11–14.15)
Globigerina soldadoensis Bronnimann, 1952, p. 7, 9, pl. 1, figs. 19
Acarinina strabocella (Loeblich and Tappan) (Figure 13.15–13.17)
Globorotalia strabocella Loeblich and Tappan, 1957, p. 195, pl. 61, figs. 6a–c.
Acarinina subsphaerica (Subbotina) (Figure 14.7–14.9)
Globigerina subsphaerica Subbotina, 1947, p. 108, pl. 5, figs. 26–28.
Acarinina wilcoxensis (Cushman and Ponton) (Figure 13.4, 13.5, 13.9)
Globorotalia wilcoxensis Cushman and Ponton, 1932, p. 71, pl. 9, figs. 10a–c.
Chiloguembelina crinita (Glaessner) (Figure 18.9–18.10)
Guembelina crinita Glaessner, 1937, p. 383, pl. 4, figs. 34a, b.
Chiloguembelina trinitatis (Cushman and Renz) (Figure 17.24–17.25)
Guembelina trinitatis Cushman and Renz, 1942, p. 8, pl. 2, figs. 8a, b
Chiloguembelina wilcoxensis (Cushman and Ponton) (Figure 18.27–18.28)
Guembelina wilcoxensis Cushman and Ponton, 1932, p. 66, pl. 8, figs. 16, 17.
Globanomalina chapmani (Parr) (Figure 13.1–13.3)
Globorotalia chapmani Parr, 1938, p. 87, pl. 3, figs. 8, 9.
Globanomalina compressa (Plummer)
Globigerina compressa Plummer, 1926, p. 135, pl. 8, figs. 11a–c.
Globanomalina ehrenbergi (Bolli) (Figure 15.18–15.20)
Globorotalia ehrenbergi Bolli, 1957, p. 77, pl. 20, figs. 18–20.
Globanomalina elongata (Glaessner)
Globanomalina pseudoscutula var. *elongata* Glaessner, 1937, p. 33, pl. 1, figs. 3d–f.
Globanomalina imitata (Subbotina) (Figure 15.13 – 15.15; 15.22–15.24)
Globorotalia imitata Subbotina, 1953, p. 206–207, pl. 16, figs. 14–16.
Globanomalina pseudomenardii (Bolli) (Figure 15.16–15.17, 15.21)
Globorotalia pseudomenardii Bolli, 1957, p. 77, pl. 20, figs. 14–17.
Igorina albeari (Cushman and Bermudez) (Figure 13.10, 13.14, 13.18)
Globorotalia albeari Cushman and Bermudez, 1949, p. 33, pl. 6, figs. 13–15.
Igorina broedermanni (Cushman and Bermudez) (Figure 18.18–18.20)
Globorotalia (Truncorotalia) broedermanni Cushman and Bermudez, 1949, p. 40, pl. 7, figs. 22–24.
Igorina pusilla (Bolli) (Figure 13.19–13.21)
Globorotalia pusilla pusilla Bolli, 1957, p. 78, pl. 20, figs. 8–10.
Igorina tadjikistanensis (Bykova) (Figure 13.11–13.13)
Globorotalia tadjikistanensis Bykova, 1953, p. 86, pl. 3, figs. 5a–c.
Morozovella acuta (Toulmin) (Figure 16.1–16.3; 16.4–16.5, 16.10)
Globorotalia wilcoxensis Cushman and Ponton var. *acuta* Toulmin, 1941, p. 608, pl. 82, figs. 68.
Morozovella acutispira (Bolli and Cita) (Figure 16.7–16.9)
Globorotalia acutispira Bolli and Cita, 1960, p. 15, pl. 33, figs. 3a–c.
Morozovella aequa (Cushman and Renz) (Figure 16.20–16.21, 16.25)
Globorotalia crassata (Cushman) var. *aequa* Cushman and Renz, 1942, p. 12, pl. 3, figs. 3a–c.
Morozovella aragonensis (Nuttall) (Figure 17.6, 17.11, 17.12)
Globorotalia aragonensis Nuttall, 1930, p. 288, pl. 24, figs. 6–11.
Morozovella angulata (White) (Figure 15.1–15.3)
Globigerina angulata White, 1928, p. 191, 192, pl. 27, figs. 13a–c.
Morozovella apantesma (Loeblich and Tappan) (Figure 16.6, 16.11, 16.12)
Globorotalia apantesma Loeblich and Tappan, 1957, p. 187, pl. 48, figs. 1a–c, pl. 55, figs. 1a–c, pl. 58, figs. 4a–c; pl. 59, figs. 1a–c.
Morozovella conicotruncata (Subbotina) (Figure 15.7–15.9)
Globorotalia conicotruncata Subbotina, 1947, p. 115–117, pl. 4, figs. 11–13; pl. 9, figs. 9–11.
Morozovella edgari (Primoli Silva and Bolli) (Figure 17.1–17.3)
Globorotalia edgari Primoli Silva and Bolli, 1973, p. 526, pl. 7, figs. 10–12, pl. 8, figs. 1–12.

- Morozovella formosa formosa* (Bolli) (Figure 17.21–17.23)
Globorotalia formosa formosa Bolli, 1957, p. 76, pl. 18, figs. 1–3.
Morozovella formosa gracilis (Bolli) (Figure 16.13–16.15)
Globorotalia formosa gracilis Bolli 1957, p. 75, 76, pl. 18, figs. 4–6.
Morozovella lensiformis (Subbotina) (Figure 17.7–17.9)
Globorotalia lensiformis Subbotina, 1953, p. 214, pl. 18, figs. 4, 5.
Morozovella marginodentata (Subbotina) (Figure 17.4, 17.5, 17.10)
Globorotalia marginodentata Subbotina, 1953, p. 212, 213, pl. 17, figs. 14–16, pl. 18, figs. 1–3.
Morozovella occlusa (Loeblich and Tappan) (Figure 16.22–16.24)
Globorotalia occlusa Loeblich and Tappan, 1957, p. 191, pl. 64, figs. 3a–c.
Morozovella subbotinae (Morozova) (Figure 15.4, 15.5, 15.10)
Globorotalia subbotinae Morozova, 1939, p. 80, pl. 2, figs. 16, 17.
Morozovella velascoensis (Cushman) (Figure 16.17–16.19)
Pulvinulina velascoensis Cushman, 1925, p. 19, pl. 3, figs. 5a–c.
Parasubbotina varianta (Subbotina) (Figure 13.6–13.8)
Globigerina varianta Subbotina, 1953, p. 63, pl. 3, figs. 5–7, 10–12.
Planorotalites pseudoscutula (Glaessner) (Figure 18.23–18.25)
Globorotalia pseudoscutula Glaessner, 1937, p. 32, figs. 3a–c.
Pseudohastigerina wilcoxensis (Cushman and Ponton) (Figure 15.6, 15.11, 15.12)
Nonion wilcoxensis Cushman and Ponton, 1932, p. 64, pl. 8, figs. 11a, b.
Subbotina inaequispira (Subbotina) (Figure 18.6–18.8)
Globigerina inaequispira Subbotina, 1953, p. 69, pl. 6, figs. 1–4.
Subbotina lozanoi (Colom) (Figure 18.1–18.3)
Globigerina lozanoi Colom, 1954, p. 149, pl. 2, figs. 1–48.
Subbotina patagonica (Todd and Kniker) (Figure 18.4, 18.5, 18.11)
Globigerina patagonica Todd and Kniker, 1952, p. 26, pl. 4, figs. 32a–c.
Subbotina prolata (Bolli) (Figure 18.12–18.14)
Globigerina prolata Bolli, 1957, p. 72, pl. 15, figs. 24–26.
Subbotina triangularis (White) (Figure 14.22–14.24)
Globigerina triangularis White, 1928, p. 195, pl. 28, figs. 1a–c.
Subbotina triloculinoides (Plummer) (Figure 14.25–14.27)
Globigerina triloculinoides Plummer, 1926, p. 134, 135, pl. 8, figs. 10a–c.
Subbotina velascoensis (Cushman) (Figure 14.16, 14.20, 14.21)
Globigerina velascoensis Cushman, 1925, p. 19, pl. 3, figs. 6a–c.
Turborotalia praecentralis Blow
Globorotalia (Turborotalia) praecentralis Blow, 1979, p. 1094, pl. 135, figs. 7–9; pl. 136, figs. 1–6; pl. 233, fig. 6.

Appendix 2: Stratigraphic distribution and relative abundance (%) of planktic foraminiferal species in the Dungan Formation exposed at the Rakhi Nala section. Here x = less than 1 %.

| Dungan Formation | | | | | | | | | | | | | | | | | | | Samples | Planktic foraminiferal species |
|------------------|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-------|--|--|---------|-----------------------------------|
| R23 | R28 | R25 | R29 | R30 | R32 | R26 | R27 | R33 | R34 | R35 | R36 | R38 | R39 | R40 | R41 | | | | | |
| | 2 | 3 | 1 | 2 | 6 | 6 | x | 1 | x | 6 | 1 | | 3 | 2 | 4 | | | | | <i>Acarinina coalingensis</i> |
| | | | | | | | | x | x | | 2 | | 1 | | 1 | | | | | <i>A. esnaensis</i> |
| | 1 | | 1 | 1 | | 2 | | | | | | | | | | | | | | <i>A. mckannai</i> |
| | 2 | 2 | 2 | 2 | 4 | 2 | 4 | 2 | | 4 | 2 | | | | | | | | | <i>A. nitida</i> |
| | | | | | | | | | | | 3 | 5 | 3 | 10 | 4 | | | | | <i>A. pentacamerata</i> |
| | | | | | | | 2 | x | 1 | 1 | 1 | 2 | 4 | 1 | 3 | | | | | <i>A. pseudotopilensis</i> |
| | | | | | | | | | | | 3 | 1 | 1 | 5 | 4 | | | | | <i>A. quetra</i> |
| | | | 10 | 3 | 13 | 11 | 14 | 18 | 8 | 28 | 22 | 25 | 31 | 36 | 19 | | | | | <i>A. sold. soldadoensis</i> |
| | | | | | | | | | | | 2 | 3 | 3 | 5 | 5 | | | | | <i>A. soldadoensis angulosa</i> |
| | 4 | | | | | | | | | | | | | | | | | | | <i>A. strabocella</i> |
| | | 1 | 1 | 1 | | | | | | | | | | | | | | | | <i>A. subsphaerica</i> |
| | | | | | | | 1 | | 3 | 13 | 11 | 4 | 6 | 4 | 7 | | | | | <i>A. wilcoxensis</i> |
| | | | 1 | | | | 1 | 1 | | | | | | | | | | | | <i>Chiloguembelina crnita</i> |
| | | | | 2 | | | | | | | | | | | | | | | | <i>Ch. trinitatensis</i> |
| | | | | | x | | | 1 | | | | | | | | | | | | <i>Ch. wilcoxensis</i> |
| | | 1 | | 1 | | | | | | | | | | | | | | | | <i>Globanomalina chapmani</i> |
| | 1 | | 2 | 3 | | | | | | | | | | | | | | | | <i>G. ehrenbergi</i> |
| | | | | | | 1 | | | | | | | | | | | | | | <i>G. elongata</i> |
| x | 1 | 1 | | 1 | x | 1 | | | | | | | | | | | | | | <i>G. imitata</i> |
| | | 2 | 8 | 14 | 1 | | | | | | | | | | | | | | | <i>G. pseudomenardii</i> |
| | | | | | | | | | | | | | | | | 5 | | | | <i>G. rakhiensis</i> |
| | 6 | | 1 | 1 | | | | | | | | | | | | | | | | <i>Igorina albeari</i> |
| | | | | | | | 1 | | 1 | 4 | 3 | 2 | 3 | 2 | 4 | | | | | <i>I. broedermanni</i> |
| | 7 | 1 | 1 | 1 | | | | | | | | | | | | | | | | <i>I. pusilla</i> |
| 3 | 4 | 3 | 4 | 4 | 4 | 3 | | | | | | | | | | | | | | <i>I. tadjikistanensis</i> |
| 46 | 9 | 58 | 14 | 17 | 33 | 23 | 9 | 11 | | | | | | | | | | | | <i>Morozovella acuta</i> |
| | | x | 1 | | x | | | | | | | | | | | | | | | <i>M. acutispira</i> |
| 4 | 6 | 2 | 1 | x | 5 | 3 | 3 | 1 | 3 | 1 | 1 | | x | | | | | | | <i>M. aequa</i> |
| 18 | 37 | 1 | | | | | | | | | | | | | | | | | | <i>M. angulata</i> |
| 3 | | 1 | 5 | 3 | | 1 | | | | | | | | | | | | | | <i>M. apantesma</i> |
| | | | | | | | | | 3 | 3 | 11 | 13 | 7 | 8 | 14 | | | | | <i>M. aragonensis</i> |
| | 2 | 5 | 3 | 2 | | 1 | | | | | | | | | | | | | | <i>M. conicotruncata</i> |
| | | | | | | | 11 | 1 | 1 | | | | | | | | | | | <i>M. edgar</i> |
| | | | | | | | | | 1 | 1 | 1 | 1 | x | x | 1 | | | | | <i>M. formosa formosa</i> |
| | | | | | 1 | 1 | 5 | 4 | 4 | 2 | 5 | | | 2 | | | | | | <i>M. formosa gracilis</i> |
| | | | | | | | | | 3 | 4 | 10 | 9 | 6 | 7 | 2 | | | | | <i>M. lensiformis</i> |
| | | | | | | | | | 6 | 6 | 2 | 2 | | 1 | | | | | | <i>M. marginodentata</i> |
| | | 3 | 4 | 2 | 1 | 5 | 2 | 5 | | | | | | | | | | | | <i>M. occlusa</i> |
| | | | | | 4 | 4 | 30 | 20 | 35 | 12 | 14 | 9 | 6 | 5 | x | | | | | <i>M. subbotinae</i> |
| | 2 | 3 | 16 | 11 | 3 | 1 | | 17 | | | | | | | | | | | | <i>M. velascoensis</i> |
| | 1 | | | | | | | | | | | | | | | | | | | <i>Parasubbotina varianta</i> |
| | | | | | | | | | | | | | 6 | 2 | 4 | | | | | <i>Planorot. pseudoscutula</i> |
| | | | | | | | 3 | 1 | 5 | 2 | 1 | 2 | 2 | | 4 | | | | | <i>Pseudohast. wilcoxensis</i> |
| | | | | | | | | | | | | 2 | 3 | 1 | 5 | | | | | <i>Subbotina inaequispira</i> |
| | | | | | | | | | | | | | | | 6 | | | | | <i>S. lozanoi</i> |
| | | | | | | | | | | 3 | | 1 | 1 | 2 | 4 | | | | | <i>S. prolata</i> |
| | | | | | | | 6 | 8 | 14 | 8 | 2 | 12 | 14 | 3 | 2 | | | | | <i>S. patagonica</i> |
| 2 | 1 | 1 | | 2 | | 3 | | | | | | | | | | | | | | <i>S. triloculinoides</i> |
| 23 | 12 | 11 | 19 | 16 | 19 | 26 | 8 | 5 | 12 | 3 | 3 | 7 | | | | | | | | <i>S. triangularis</i> |
| | 3 | 3 | 7 | 7 | 5 | 9 | x | 1 | | | | | | | | | | | | <i>S. velascoensis</i> |
| | | | | | | | | | | | | 3 | | | | | | | | <i>Turborotalia praecentralis</i> |
| 226 | 393 | 308 | 383 | 409 | 291 | 343 | 316 | 288 | 305 | 187 | 262 | 199 | 304 | 243 | 301 | | | | | Total Counts |
| 8 | 18 | 19 | 20 | 22 | 15 | 18 | 17 | 19 | 16 | 17 | 20 | 18 | 19 | 18 | 20 | | | | | Species Number |
| P3B | | | P4A | P4B | P5 | P7 | | | | | | | | | | Zones | | | | |

Appendix 3: Stratigraphic distribution and relative abundance (%) of planktic foraminiferal species in the Dungan Formation exposed along the eastern and western limbs of the Zinda Pir Anticline. Here x = less than 1 %.

| Dungan Formation | | | Western side | | | | | | | | | | Eastern side | | | | | | | | | | Total Counts | Species Number | Zones | | | | | | | | | | | | | | |
|--------------------------------------|--|--|-------------------------------------|--------|-----|--------|-----|--------|-----|--------|-----|--------|--------------|--------|-----|--------|-----|--------|-----|--------|----|-------|--------------|----------------|-------|-------|----|--------|----|--------|----|--------|----|--------|----|--------|----|--------|--|
| | | | Samples | ZPW-22 | | ZPW-21 | | ZPW-20 | | ZPW-19 | | ZPW-18 | | ZPW-17 | | ZPW-16 | | ZPW-15 | | ZPW-13 | | ZPW-5 | | | | ZPW-1 | | ZPE-26 | | ZPE-20 | | ZPE-19 | | ZPE-18 | | ZPE-16 | | ZPE-15 | |
| Planktic foraminiferal Species | | | <i>Acaritina coalingensis</i> | 1 | | 2 | 9 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | | | <i>A. mckennai</i> | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | | | <i>A. nitida</i> | 2 | 9 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | | | <i>A. soldadoensis soldadoensis</i> | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | | | <i>A. strabocella</i> | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | | | <i>A. subsphaerica</i> | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | | | <i>A. wilcoxensis</i> | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | | | <i>Globanomalina chapmani</i> | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | | | <i>G. compressa</i> | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | | | <i>G. ehrenbergi</i> | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | | | <i>G. imitata</i> | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | | | <i>G. pseudomenardii</i> | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | | | <i>Igorina albeari</i> | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | | | <i>I. pusilla</i> | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| <i>I. tadjikistanensis</i> | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| <i>Morozovella acuta</i> | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| <i>M. acutispira</i> | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| <i>M. aequa</i> | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| <i>M. angulata</i> | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| <i>M. apantesma</i> | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| <i>M. conicotruncata</i> | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| <i>M. formosa gracilis</i> | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| <i>M. occlusa</i> | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| <i>M. subbotinae</i> | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| <i>M. velascoensis</i> | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| <i>Parasubbotina varianta</i> | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| <i>Pseudohastigerina wilcoxensis</i> | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| <i>Subbotina trilobulinoides</i> | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| <i>S. triangularis</i> | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| <i>S. velascoensis</i> | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | | | 361 | 250 | 271 | 284 | 278 | 264 | 267 | 313 | 79 | 67 | 5 | 352 | 191 | 166 | 69 | 112 | 178 | 367 | 15 | 18 | 18 | 16 | 20 | 18 | 17 | 7 | 13 | 4 | 15 | 14 | 15 | 14 | 18 | 19 | 20 | | |
| | | | Species Number | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | | | Zones | | P5 | | P4B | | P4A | | P3B | | P3A | | P5 | | P4B | | P4A | | | | | | | | | | | | | | | | | | | | |

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行 事 予 定

- ◎第150回例会は、2001年1月27日(土)と28日(日)に「茨城県自然博物館」で開催されます。27日にシンポジウム「新生代軟体動物古生物学の最近の動向(世話人:野田浩司・天野和孝・島本昌憲・間嶋隆一)」が行われます。個人講演の申し込み締切日は2000年12月1日(金)です。
- ◎2001年年会・総会は、2001年6月29日(金)、6月30日(土)、7月1日(日)に「国立オリンピック記念青少年総合センター」で開催されます。21世紀最初の年会ですので、「21世紀の古生物学」を統一テーマとし、29日に統一シンポジウム、30日と1日に17件の課題別シンポジウムが行われる予定です。現在、学会の「将来計画委員会」によってプログラムの詳細を立案中です。一般講演はポスター講演だけに限って受け付けます。口答発表形式による一般講演はありませんのでご注意ください。ポスター講演の申し込み締切日は2001年5月9日(水)です。
- ◎第151回例会(2002年1月下旬開催予定)には鹿児島大学理学部からの開催申し込みがありました。
- ◎2002年年会・総会(2002年6月下旬開催予定)には福井県立博物館から開催申し込みがありました。
- ◎古生物学会では、小人数で実施されるワークショップやショートコースを主催しております。学会から金銭を含む援助を行なうことができますので、企画をお持ちの方は行事係までお問い合わせ下さい。

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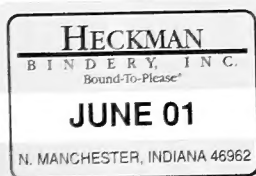
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